University of Alberta

THE EFFECTS OF FOREST FRAGMENTATION ON PARASITOIDS OF THE FOREST TENT CATERPILLAR (*MALACOSOMA DISSTRIA*)

by

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ABSTRACT

The forest tent caterpillar (*Malacosoma disstria*, (Hübner)) is a cyclic defoliator of trembling aspen (*Populus tremuloides*) found throughout most of North America. The cyclic dynamics of this species are believed to be linked to parasitoids. In this study I experimentally elevate FTC density in both forest fragments and continuous forest and examine resultant parasitism to gain insight into the effect of fragmentation on parasitoid movement. I also examine the effects of forest fragmentation on the structure of the late larval FTC tachinid parasitoid community.

For most species, parasitism rates did not differ significantly between forest fragments and continuous forest, for the remainder, parasitism was higher in fragments. There was no effect of isolation distance, landscape connectedness, nor patch size on parasitism. Forest fragmentation did affect the relative abundance of FTC parasitoid species, however, parasitoid communities in individual forest fragments were similar to that found in continuous forest.

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Table of Contents

1 Introduction 1

Bibliography 7

2 The effect of forest fragmentation on parasitism - an experimental approach 11

Introduction 12

Methods 18

Study area 18

Experimental manipulation of host densities 21

Sampling 22

Rearing 23

Estimates of mean instar 24

Host density estimates 25

Site characteristics 25

Statistical analysis 26

The effect of fragmentation on parasitism 27

Additional effects of isolation and patch size 29

Edge effects on parasitism and FTC development 30

Additional site effects 31

Results 32

Effects of fragmentation on parasitism 33

Edge effects on parasitism and host development 40

The effect of site characteristics on parasitism 42

Discussion 45
Bibliography 57

3 The effect of landscape and host density on the late larval parasitoid assemblage of the forest tent caterpillar (*Malacosoma disstria*) 63
Introduction 64
Methods 71
Collection methods and rearing 71
Statistical analysis 73
Results 78
Collections 78
Host density 78
Geographic location 89
Discussion 91
Bibliography 102

4 Conclusion 107
Bibliography 113

List of Figures

2.1 Location of the two reserves used in this study. Black Bear Grazing Reserve, (54.5/114'), located 45 km west of Athabasca, Alberta. Blackfoot Grazing Reserve near Cooking Lake, Alberta (N53/112 W). White arrows show pairing of forest fragment with continuous forest. 19

2.2 Schematic of paired experimental design. Host density was elevated in both a forest fragment, and a corresponding tract of continuous forest. Fragment-continuous pairings are represented by "Blocks". 20

2.3 Histogram of the distribution of parasitism by a) *L. frenchii*, b) *C. malacosomae*, and c) *A. aldrichi* from both the Blackfoot and Black Bear reserves. N = the number of sites in each reserve. 28

2.4 The effect of landscape structure on the proportion of forest tent caterpillar parasitized by a) late larval and b) pupal parasitoids. The dark line represents the median, with the surrounding box showing the interquartile range. Whiskers show range of all values which are not classified as outliers. o = outliers in 1.5-3.0 box lengths from upper or lower edge of box. * = points which are greater than 3 box lengths from upper or lower edge of box. 37

2.5 The effect of landscape structure on the proportion of hosts parasitized by a) *L. frenchii*, b) *C. malacosomae*, and c) *A. aldrichi* in both 2003 and 2004. Plot as in Fig 2.4 38

2.6 Spline fit of the effects of isolation distance on parasitism by *L. frenchii*. Dotted line shows standard error. 39

2.7 Parasitism by *C. malacosomae* at the edge and interior of forest stands. Plot as in Fig. 2.4 40

2.8 Spline fit of the effect of *Shepherdia canadensis* abundance on parasitism by *L. frenchii*. Dotted line shows standard error. 43

3.1 Schematic showing that spatial replication was necessary to get full range of host densities. Endemic data were collected from the Black Bear Grazing reserve (10 sites), and the Blackfoot Grazing Reserve (8 sites). Outbreak data were collected from the Ministik area (including Blackfoot Grazing Reserve) near Cooking lake Alberta (130 sites). . . 72

3.2 Changing community composition of the FTC late larval parasitoid community over a 10 year period in the Cooking Lake region of Alberta. 1995=Initial Outbreak, 1996=Peak Outbreak, 1998=Collapse, 2002-2004=endemic host densities. 81

3.3 Community structure of FTC parasitoid communities from sites with differing levels of fragmentation. N = total number of parasitoids collected. 85

3.4 Late larval tachinid parasitoid community structure for forest fragments and continuous forest N= total number of parasitoids collected. 86

3.5 Late larval tachinid community structure for both the Blackfoot and Black Bear reserve. Both reserves were at low host densities at the time of these collections. N= total number of parasitoids collected. . 90

List of Tables

2.1 Key members of the parasitoid community from low density host populations within the Black Bear and Blackfoot Grazing Reserves. The "Phase specialty" refers to the stage of the host cycle during which parasitism is greatest for a given parasitoids species. 17

2.2 Parasitoid species identified from the Black Bear and Blackfoot reserve. Proportion of hosts parasitized was calculated as number of parasitoids collected divided by total number of larvae (or pupae) collected. Total larvae colected = 942, Total pupae collected = 409. 33

2.3 Generalized linear mixed-effects model of overall larval and pupal parasitism in forest fragments and continuous forest. For fixed effects I provide type 3 F-statistics with associated df and P values. For random effects, I provide covariance parameters and associated standard errors. 34

2.4 Generalized linear mixed-effects model of parasitism in forest fragments and continuous forest for three FTC parasitoids. Format as in Table 2.3 35

2.5 Coefficient and the associated significance of the linear, non-linear spline, and exponential fit of the effect of patch size, isolation, and connectedness on parasitism by three species of FTC parasitoids. . . 36

2.6 Generalized linear mixed-effects model of the effects of proximity to forest edge and of forest structure on parasitism by three FTC parasitoids. Format as in Table 2.3 41

2.7 Repeated measures mixed-effects model of FTC maturation rate in forest fragments and continuous forest. Format as in Table 2.3 42

2.8 Coefficient and the associated significance of the linear, non-linear spline, and exponential fit of the effect of abundance of *S. canadensis*, percent canopy cover, and abundance of aspen on parasitism by three species of FTC parasitoids. 44

3.1 Members of the forest tent caterpillar late larval tachinid parasitoid community. The "Instar of emergence" refers to the instar from which the parasitoid leaves the host. "Mode of parasitism" refers to whether parasitoids lay eggs directly on hosts, or on the surrounding foliage (for host ingestion). "Phase specialty" refers to the phase of the host cycle during which that species was most prominent with respect to abundance and percent parasitism 70

3.2 MRPP analyses and species diversity values for differing stages of the host cycle. For MRPP; N = the number of samples in each group. A = change-corrected within-group agreement. P= significance level for the differences between groups. Outbreak(Sub1-3) represent sub-samples of sites from the outbreak sample area. Each subgroup was comprised of sites from a 12 x 8 km sample area within the larger outbreak sample area (Ministik and Blackfoot Grazing Reserve). Outbreak(SubFragClass) represents a sub-sample of only those sites with 0-75% forest cover. For Simpson index; D = index of diversity. For each analysis, two years of data were combined for each site. 79

3.3 Results from Indicator Species Analysis for differing phases of the host cycle. Indicator values represent % of perfect indication, based on combination of relative abundance and relative frequency. P values represent the Monte Carlo significance of each observed indicator value based on 1000 randomizations; P values are based on the proportion of randomized trials where indicator values were equal to, or exceeded, the observed indicator value (McCune & Mefford, 1999). 80

3.4 MRPP analyses and species diversity values for the outbreak parasitoid community in landscapes with differing degrees of forest fragmentation. Format as in Table 3.2 83
3.5 MRPP analyses and species diversity values for the low host density parasitoid community in landscapes with differing degrees of forest fragmentation. Format as in Table 3.2 84
3.6 MRPP analyses and species diversity values for parasitoid communities in forest fragments and continuous forest. Format as in Table 3.2 . . 84
3.7 Results from Indicator Species Analysis for the outbreak parasitoid community found in forests with differing degrees of fragmentation. Format as in Table 3.3 87
3.8 Results from Indicator Species Analysis for the endemic parasitoid community found in forest with differing degrees of fragmentation. Format as in Table 3.3 87
3.9 Results from Indicator Species Analysis for the endemic parasitoid community found in forest fragments and continuous forest. Format as in Table 3.3 88
3.10 MRPP analyses and species diversity values for parasitoid communities in the Black Bear Grazing Reserve, and the Blackfoot Grazing Reserve. Format as in Table 3.2 89

Chapter 1

Introduction

The forest tent caterpillar (*Malacosoma disstria* Hübner) is a univoltine, cyclic defoliator of trembling aspen (*Populus tremuloides* Michx.) that is found throughout North America (Fitzgerald, 1995). Outbreaks of this species have been reported as early as 1797 (Hodson, 1941), and typically occur approximately every 14 years, with outbreaks lasting between 2 and 6 years (Sippel, 1962). FTC outbreaks are the largest of any insect species found in the United States, and larval densities can reach upwards of 750 000 individuals per hectare (Batzer *et al.*, 1995). In Canada, outbreaks have resulted in defoliation of areas as large as 190 000 km^2 (Ontario in 1991) (Roland, 1993). Although outbreaks of this species are known to be particularly damaging amongst cyclic defoliators (Witter, 1979), FTC defoliation is rarely the primary cause of tree death (Hildahl & Reeks, 1960). Defoliation can reduce tree growth and increase susceptibility to disease (Fitzgerald, 1995), making a full understanding of the factors affecting FTC outbreaks of both ecological and economic interest.

The cyclic dynamics of forest defoliators are believed to be driven by a combination of factors such as weather (Blais *et al.*, 1955; Myers, 1998; Peltonen *et al.*, 2002), intrinsic factors related to host density such as maternal effects (Rossiter, 1994), predators (Liebhold *et al.*, 2000), and/or disease (Myers, 2000; Rothman & Roland, 1998). As well, cyclic dynamics can be driven by parasitoids (Berryman, 1996). The potential for parasitoids to affect host dynamics makes them a particularly well studied group often used as biocontrol agents. In order to efficiently use parasitoids in this role, however, we must understand how they respond to the landscape in which they are found.

Forest fragmentation is one of the primary anthropogenic disturbances threatening forests worldwide, resulting in loss of habitat, increase in forest edge, and decreased

connectivity for forest dwelling animals (Saunders *et al.*, 1991). The response of parasitoids to fragmentation is of notable interest because theory predicts that parasitoids should be more strongly affected by fragmentation than are their hosts due to the high trophic level which they occupy (Davies *et al.*, 2000; Kruess & Tscharntke, 2000; Steffan-Dewenter, 2003; Thies *et al.*, 2003). FTC outbreaks are of longer duration in fragmented forest than in continuous forest (Roland, 1993), and this has been attributed to the inhibitory impact of fragmentation on parasitoid movement while foraging for hosts. Parasitoids must move to forage, aggregating in areas of high host density (Gould *et al.*, 1990; Liebhold & Elkinton, 1989; Parry *et al.*, 1997). In doing so, they may help maintain host populations at endemic levels by suppressing incipient outbreaks (Liebhold & Elkinton, 1989; Maron *et al.*, 2001; Maron & Harrison, 1997). However, if forest clearings inhibit parasitoid movement, then hosts in isolated forest stands may experience reduced parasitism compared to those in continuous or highly connected forest. Fragmentation may thus decouple parasitoids from their hosts, potentially resulting in the "release" of low density host populations at some sites (Brodmann *et al.*, 1997; Davies *et al.*, 2000; Maron & Harrison, 1997; Maron *et al.*, 2001; Thies *et al.*, 2003).

Studies of the effect of fragmentation on parasitism are primarily descriptive, and there has been little work examining the mechanisms responsible for these effects. The difficulty lies in teasing apart parasitoid movement (in response to host density), from the numerical increase of parasitoids over time. That is, patterns of parasitism in the landscape are likely to reflect both parasitoid movement, and the accumulation of parasitoids in a site over time. When host densities are low, however, it is likely that parasitoids will be sparsely distributed in the landscape. Parasitism in experi-

mentally elevated host populations will therefore at least partially reflect a parasitoid aggregative response. By creating high density patches of hosts in both forest fragments and continuous forest, one can compare parasitism and attempt to infer the ability of parasitoids to move through the landscape. That is, if parasitism is lower in forest fragments compared to connected forest, we can infer that parasitoids are unable to move throughout the agricultural landscape with the same efficiency with which they move through natural forest.

Despite the scarcity of experimental studies examining the mechanisms responsible for fragmentations effects, there are even fewer studies examining how parasitoid communities as a whole are affected by fragmentation. FTC parasitoid species are known to respond to fragmentation in a size dependent manner (Roland & Taylor, 1997), with parasitism by small parasitoids related most strongly to fragmentation when measured at small spatial scales, while larger parasitoids responding most strongly to landscape at a larger spatial scale. Furthermore, although the majority of FTC parasitoids respond negatively to fragmentation, some species respond positively. These differential responses to fragmentation may result in the abundance of parasitoid species relative to each other being altered in fragmented landscapes. Parasitoid communities of cyclic defoliators are also likely to differ in species composition between outbreak and endemic host populations (Embree, 1966; Fuester *et al.*, 1983; Hoch *et al.*, 2001; Miler & Renault, 1976; Mills, 1990). Given that the parasitoid response to fragmentation is species specific, we might also expect parasitoid communities from high and low host density populations to differ in their responses to forest fragmentation. Unfortunately most studies of parasitoids are from high-density host populations due to the inherent difficulty at working in low density host pop-

ulations. Yet an understanding of the effects of anthropogenic landscape change on host-parasitoid dynamics during both FTC outbreaks and the endemic stage of the host cycle is necessary if we are to properly manage and conserve parasitoid function (Skinner *et al.*, 1993).

Although FTC are attacked by both hymenopteran and dipteran parasitoids, I focus on the effects of landscape on dipteran parasitoids, which are not as well studied as hymenopteran, but which account for approximately 20% of all parasitoid species (Feener Jr. & Brown, 1997). The effect of landscape on dipteran parasitoids is of particular importance as they are the dominant parasitoids of externally feeding (exophytic) hosts (Stireman & Singer, 2003), and are therefore particularly relevant with respect to cyclic defoliators. Furthermore, the findings of studies on hymenopteran parasitoids are often not applicable to dipterans because of key differences in life history characteristics (see Belshaw (1994), Eggleton & Belshaw (1993), and Feener Jr. & Brown (1997) for a review of dipteran parasitoids). For example, dipteran parasitoids typically do not have piercing ovipositors, but instead lay eggs on the external surface of the hosts, or on the surrounding foliage (Belshaw, 1994). Perhaps because of this, dipteran parasitoids are typically more polyphagous than are their hymenopteran counterparts (Belshaw, 1994; Feener Jr. & Brown, 1997), and may therefore respond differently to changes in host abundance.

In the Chapter 2 of this thesis, I examine the effects of forest fragmentation on the movement of three FTC parasitoids; *Lespesia frenchii* (Williston), *Carcelia malacosomae* Sellers, and *Arachnidomyia aldrichi* (Parker). By experimentally manipulating host density and monitoring the parasitoid response, I indirectly assess whether fragmentation at the scale found in the agricultural landscape of Alberta reduces

parasitoid movement. I use the within-generation response of parasitoids to elevated host density (see Gould *et al.* 1990, Elkinton *et al.* 1990) to examine if parasitoid movement is inhibited by forest clearings, and if this results in lower parasitism in isolated forest fragments. I predict that parasitism will be lower in forest fragments because parasitoids will move less efficiently through the matrix surrounding isolated forest fragments than they will through equivalent distances of natural aspen forest.

In Chapter 3, I evaluate how landscape and host abundance affect the composition of the FTC late larval tachinid parasitoid community. Specifically, I compare parasitoid communities from the high and and low density phase of the population cycle, from landscapes with differing amounts of forest fragmentation, and finally between two geographically different locations with Alberta (140 km apart). I also examine how the effects of landscape on the FTC parasitoid community is dependent upon host density. That is, does fragmentation have a stronger effect on parasitoid complexes from high or low density host populations? In doing so, I aim to gain understanding of the nature of host-parasitoid spatial and temporal dynamics.

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Chapter 2

The effect of forest fragmentation on parasitism - an experimental approach

Introduction

Forest fragmentation is one of the primary anthropogenic disturbances threatening forests worldwide, resulting in loss of habitat, decreased connectivity for forest dwelling animals, and high amount of forest edge (Saunders *et al.*, 1991). These alterations to the landscape can result in community level changes by impacting multi-species interactions and movement-dependent processes such as pollination and predation (Aizen & Feinsinger, 1994; Kruess & Tscharntke, 2000; Ryall & Fahrig, 2005; Tscharntke *et al.*, 2002; With *et al.*, 2002). Of particular interest for the boreal forests of North America is how forest fragmentation affects the interaction between cyclic forest defoliators and their natural enemies.

The forest tent caterpillar, *Malacosoma disstria* Hübner (FTC), is one of the primary cyclic defoliators of Alberta's boreal forests. This species has periodic population outbreaks approximately every 14 years (in Ontario), with outbreaks lasting between 2-6 years, although periodicity and duration of outbreaks do differ among regions (Sippel, 1962). Although the cycle is likely affected by a combination of weather (Blais *et al.*, 1955; Myers, 1998; Peltonen *et al.*, 2002), various endogenous factors such as maternal effects (Rossiter, 1994), and viral disease (Rothman & Roland, 1998), it is felt by others that the underlying cycle is driven by natural enemies including parasitoids (Berryman, 1996). Many parasitoids have co-evolved with a few species of hosts, resulting in a tight "predator-prey" linkage (Godfray, 1994). Host specificity, coupled with the ability of parasitoids to respond numerically to host density allows FTC parasitoids to cause high levels of mortality during host outbreaks, potentially leading to collapse of host populations (Fitzgerald, 1995; Parry *et al.*, 1997; Sippel,

1962; Witter & Kulman, 1979). Forest tent caterpillar outbreaks last longer in fragmented forest, and this may result from the negative impact of fragmentation on parasitoids (Roland, 1993). The impact of fragmentation on FTC parasitoids is thus of both economic and scientific interest. This is particularly so given that both empirical (Kruess & Tscharntke, 2000; Thies *et al.*, 2003) and theoretical (Davies *et al.*, 2000; Holt *et al.*, 1999) studies indicate that the effects of fragmentation are stronger on parasitoids than on their herbivorous hosts.

Forest fragmentation may impact FTC parasitoids negatively by reducing their movement while foraging for hosts (Roland, 1993). Parasitoids must move to forage, aggregating in areas of high host density (Gould *et al.*, 1990; Liebhold & Elkinton, 1989; Parry *et al.*, 1997). By doing so, they may help maintain host populations at endemic levels by suppressing incipient outbreaks (Liebhold & Elkinton, 1989; Maron *et al.*, 2001; Maron & Harrison, 1997). If forest clearings inhibit the movement of forest dwelling parasitoids, then hosts in isolated forest stands may experience reduced parasitism compared to those found in continuous or highly connected forest. Fragmentation may thus decouple parasitoids from their hosts, potentially resulting in the "release" of low density host populations at some sites (Brodmann *et al.*, 1997; Davies *et al.*, 2000; Maron *et al.*, 2001; Maron & Harrison, 1997; Thies *et al.*, 2003). Furthermore, theoretical work has shown that altering the aggregation ability of parasitoids can affect the stability of host-parasitoid systems (Godfray & Pacala, 1992; Rohani *et al.*, 1994; Rohani & Miramontes, 1995). For logistical reasons, many host-parasitoid studies ignore parasitoids in endemic host populations, focusing instead on their role in causing collapse of FTC outbreaks. Although research during outbreaks is important, we must also fully understand the effects of anthropogenic landscape

change on host-parasitoid dynamics in endemic host populations if we are to properly manage and conserve parasitoid function (Skinner *et al.*, 1993). This is particularly important as the biotic factors affecting parasitoids in outbreak populations of cyclic defoliators differ from those impacting low density populations (Liebhold *et al.*, 2000).

In the boreal forests of Alberta, the complex of parasitoids that attack forest tent caterpillar larvae is comprised of flies of the family Tachinidae and Sarcophagidae, and parasitic wasps of the family Ichneumonidae and Braconidae. However, dipterans typically dominate the FTC parasitoids complex. Tachinid flies attack FTC's late-larval stages, while sarchophagid flies cause high levels of pupal mortality (Parry *et al.*, 1997; Sippel, 1962; Witter & Kulman, 1979). The composition of parasitoid communities can differ between regions (Parry *et al.*, 1997; Stark & Harper, 1982), as well as between endemic and epidemic stages of the cycle (Parry *et al.*, 1997; Sippel, 1962). Forest tent caterpillar parasitoids differ not only in the stage at which they attack, but also in a variety of other characteristics (see Table 3.1). Parasitism by *Carcelia malacosomae* Sellers and *Lespesia frenchii* (Williston) (Tachinidae) is greater in endemic host populations (and in the case of *L. frenchii* during outbreak collapse) than during FTC outbreaks (Parry *et al.*, 1997; Sippel, 1962). This is likely because these two generalist parasitoids are overwhelmed when host densities are high by those parasitoid species showing numerical increases in response to in host density, such as *Leschenaultia exul* (Townsend) and *Patelloa pachypyga* (Aldrich and Webber). Although both *L. frenchii* and *C. malacosomae* are present in many FTC populations, they do not exhibit a density-dependent response to host populations, and are therefore unlikely to affect host dynamics (Parry, 1995). This is in contrast to *Arachnidomyia aldrichi* (Parker) (Sarcophagidae), the most common pupal parasite

in the both the Lake States and prairie provinces (Witter, 1979), which is believed to play a particularly important role in host population collapse causing parasitism of more than 80% during FTC outbreaks (Hodson, 1939; Parry, 1995; Sippel, 1962).

Despite the number of theoretical and descriptive studies on the potential impacts of fragmentation on parasitoid movement (see above), there is little experimental work examining the details of this mechanism. The difficulty lies in teasing apart parasitoid movement (in response to host density), from the numerical increase of parasitoids over time. That is, patterns of parasitism in the landscape are likely to reflect both parasitoid movement into an area, and the accumulation of parasitoids within a site over time. When host densities are low, however, it is likely that parasitoids will be sparsely distributed in the landscape. I therefore assume that the response of parasitoids to locally elevated host density will at least partially depend on parasitoid movement. In this study I experimentally elevated local host density in two years in both highly connected tracts of continuous forest and forest fragments, and monitor the within-generation parasitoid response (parasitism rate) in order to indirectly gain insight into whether fragmentation at the scale of the experiment negatively impacts parasitoid movement. By creating point sources of high host density in endemic populations of FTC, I maximize the contrast between patches of experimentally elevated host density and the surrounding area, thereby eliciting a parasitoid aggregative response (Elkinton *et al.*, 1990). Experimental population elevation of defoliating insects has been done successfully with other Lepidoptera, with spatial density-dependent responses reported by the parasitoids of gypsy moth (*Lymantria dispar* Linnaeus) (Gould *et al.*, 1990) and forest tent caterpillar (Parry *et al.*, 1997). I hypothesize that the stretches of agricultural land separating fragments from con-

tinuous forest will inhibit the movement of forest dwelling parasitoids and result in reduced parasitism in local outbreaks in forest fragments. This effect is expected to be most pronounced for smaller parasitoids due to the potential relationship between body size and dispersal ability (Roland & Taylor, 1997).

Table 2.1: Key members of the parasitoid community from low density host populations within the Black Bear and Blackfoot Grazing Reserves. The "Phase specialty" refers to the stage of the host cycle during which parasitism is greatest for a given parasitoids species.

Species	**Size (mg)**[b]	**# Alternative Host Species**[c]	**Phase Specialty**	**# Generations per year**[e]
C. malacosomae	34	8	endemic[a]	1
L. frenchii	<34	48	declining[a], endemic[a f]	2
A. aldrichi	58	6	all stages	1

[a] (Parry, 1995)
[b] (Roland & Taylor, 1997)
[c] (Schmidt, 2001)
[d] (Sippel, 1962)
[e] (Williams *et al.*, 1996)
[f] (Witter & Kulman, 1979)

Methods

Study area

Experimental outbreaks were created at two sites: the Black Bear Grazing Reserve (54.5 N/114'W) located 45 km west of Athabasca, Alberta (Fig. 2.1), and the Blackfoot Grazing Reserve near Cooking Lake, Alberta (N53/112 W). The use of two reserves was not an attempt to examine large scale landscape differences between reserves, but was done to increase the number of standardized pairs of connected and un-connected aspen forest, and because both reserves contain large tracts of continuous forest surrounding a heavily fragmented interior (Fig. 2.1). This structure allows for the pairing of forest fragments and continuous forest in close proximity (Fig. 2.2). Forest fragments used in this study range in size from 0.76ha to 5ha, and were isolated from the nearest continuous forest by between 400m and 1400m. Experimental FTC outbreaks were created in the same 12 sites in both years due to the logistical difficulty in finding suitable sites. Five pairs were located in the Black Bear Grazing Reserve, and one pair was in the Blackfoot Grazing Reserve.

The most recent FTC outbreak occurred at the Black Bear Grazing Reserve approximately 17 years prior to this experiment (1988), while the Blackfoot Grazing Reserve experienced its last outbreak approximately 8 years prior (1997). Areas with low FTC density were chosen in order to allow for maximum contrast between experimentally created outbreaks and background density. The background density of FTC remained low throughout the experiment in both reserves, although pheromone trap data from the region (Roland unpublished data) suggest that the tent caterpillar at Black Bear reserve may be entering the early stages of a new outbreak.

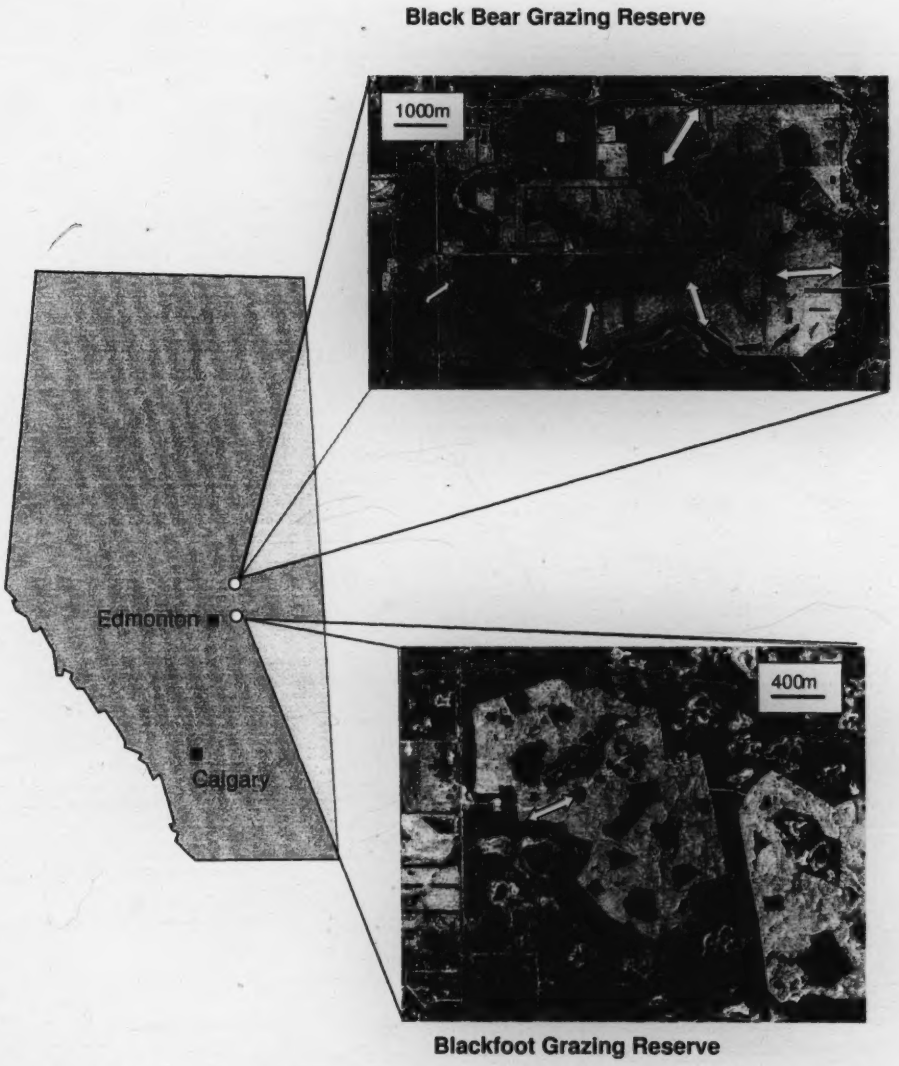

Figure 2.1: Location of the two reserves used in this study. Black Bear Grazing Reserve, (54.5/114'), located 45 km west of Athabasca, Alberta. Blackfoot Grazing Reserve near Cooking Lake, Alberta (N53/112 W). White arrows show pairing of forest fragment with continuous forest.

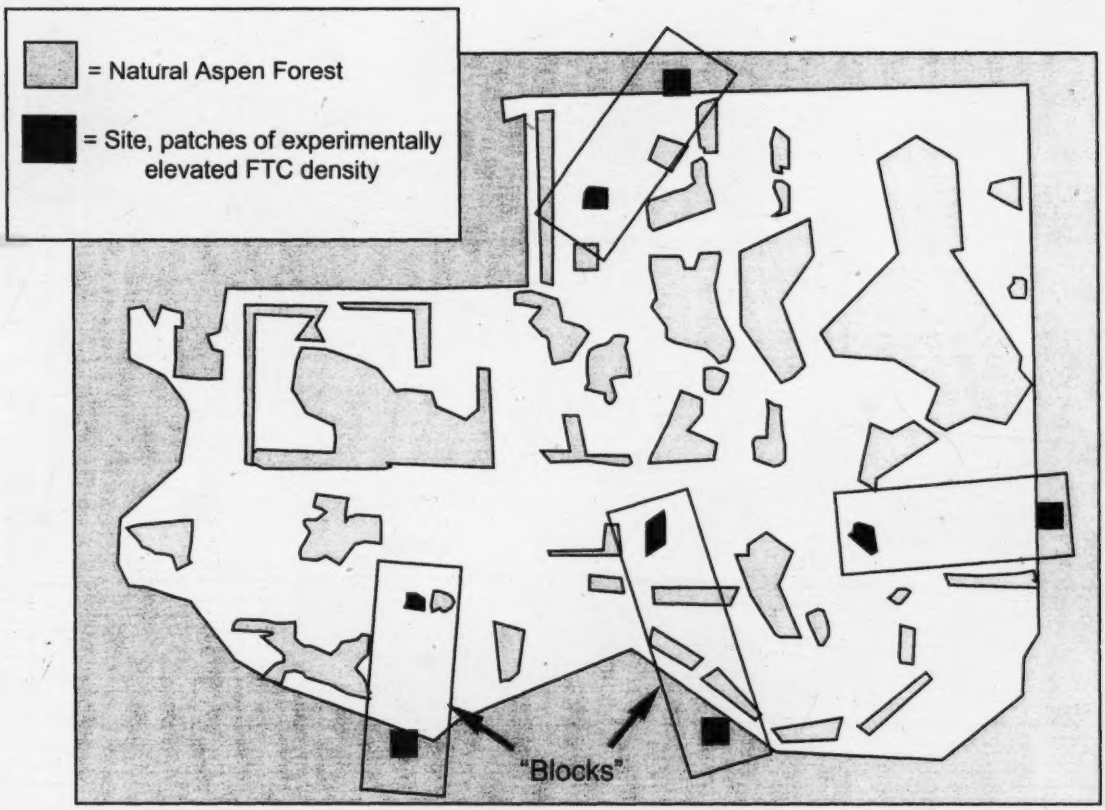

Figure 2.2: Schematic of paired experimental design. Host density was elevated in both a forest fragment, and a corresponding tract of continuous forest. Fragment-continuous pairings are represented by "Blocks".

Experimental manipulation of host densities

FTC densities were elevated by transplanting egg masses from a pre-existing FTC outbreak to my sites. Egg masses were collected from high-density populations near Rocky Mountain House, Alberta (52.43 N/ 114.93 W) from December through April in 2002-2004. Terminal twigs bearing egg masses were clipped 1-2 inches from the egg mass to allow for easy placement on experimental trees. Approximately 6500 egg masses were collected in each year, and were kept at ambient outdoor temperature until spring. In 2003, egg masses were soaked for 1 min in a 10 percent bleach solution prior to release in order to remove surface Nuclear Polyhedrosis virus. Egg masses were not bleached in 2004 because of the ineffectiveness of the bleaching treatment in 2003, and the potential for the bleaching treatment to damage the eggs. Five hundred egg masses were placed in each fragment and continuous tract of forest in both the Black Bear and Blackfoot Grazing Reserves (six fragments and six continuous). Sites in each reserve were chosen on the basis of forest composition, tree size, and access. Fragments were paired with a nearby tract of continuous forest in order to allow for pairwise analyses, since there may have been background gradients of parasitoid density, host density, and habitat quality (Fig. 2.2). Outbreaks were created on the edge of both forest fragments and continuous forest in an attempt to control for potential edge effects (Roland, 2000).

Attempts were made to plant egg masses prior to aspen bud break, but an unusually early spring during 2003 forced me to plant egg masses during, or slightly after, the initiation of bud break. Egg masses were attached close to the terminal buds of three-to-five meter tall aspen to ensure access to food for hatching larva. Three-to-

six egg masses were placed per tree depending on tree size, with more egg masses attached to larger trees. Egg masses were distributed throughout the tree with no more than one egg mass per branch. Egg masses were distributed evenly throughout each 50 X 70m site, although the distribution of egg masses was constrained by the distribution of appropriate aspen trees. One of the continuous sites in 2003 ended up being approximately 90x50m in area because of the low density of trees. In 2004, the number of egg masses per tree was increased in this site to ensure an area of 50x70m. A five inch strip of Tangle foot (Tanglefoot, Grand Rapids, Michigan, USA) was applied around the trunk of all aspen trees in 2004 in an attempt to improve FTC survival by excluding ants.

Sampling

Sampling of FTC was carried out twice during the summer to estimate both late larval and pupal parasitism (Witter & Kulman, 1979). Early-instar larvae were not sampled as such a collection would limit the quality of estimates for late-instar and pupal parasitism due to low host density, and because parasitoids attacking early-instars are neither abundant, nor thought to be important in determining FTC dynamics.

Late-instar larvae were sampled over a 10-14 day period in late June and early July. Populations were monitored twice weekly to determine when the majority of hosts had entered 5th instar, after which collections began. In 2003, sites within a block were sampled twice, and at most 3 days apart. Two collections were made in order to increase sample size. In 2004, I was forced to adopt a more opportunistic sampling regime because of greater differences in host developmental rates within sites, as well as between sites within a block, and because of extremely low host densities. Each site

was sampled on three or four separate occasions, with the sampling period between sites in a block varying at most by 5 days. The order of sampling was determined by host phenology. Only late fifth instar larvae were collected during each sampling period in order to ensure that parasitoids were given an equal opportunity to parasitize hosts in all sites. Collections were classified as edge or interior depending on whether larvae were collected at less than 15m, or greater than 15m, from the forest edge. This stratification was done because tachinid parasitism is low near the forest edge, but levels off after approximately 20m (Parry, 1994; Roland, 2000).

Pupal collections were carried out in a similar manner. In 2003 one and a half hours were spent per site, with additional time if numbers were low. In 2004, two separate collections were made one week apart due to the wide range of pupation dates. The first collection occurred 5 days after the first pupa was seen in the site, and the second collection was made one week later. Understory shrubs, and small aspen trees in each site were searched, and two to five large trees were cut down per site in order to collect cocoons from the canopy. Those trees that were cut were chosen primarily based upon the ease and safety with which they could be cut. All cocoons were placed in paper bags labeled by site and proximity to edge (edge vs. interior).

Rearing

Larvae were reared in paper bags and fed fresh aspen foliage every two days. The number of larvae in each bag was kept as low as possible to minimize rearing mortality. Larvae were reared until healthy FTC adults, or parasitoids emerged. Mortality of FTC during rearing was recorded as being due to either parasitism, virus, or unknown

causes, with dead larvae removed in order to reduce the risk of disease.

Pupae were kept in paper bags until host/parasitoid emergence, after which all pupae were dissected to determine any additional parasitism. Parasitoids were identified using puparium characteristics (Sippel, 1956), with parasitized hosts identified on the basis of either a dried FTC mummy, or parasitoid puparium on the outer silk layer of the host pupa. Healthy hosts were identified by the presence of an adult moth, or by the presence of a dried paper-like puparium and characteristic split exit hole.

Rates of parasitism were estimated from the number of emerged parasitoids found in each sample bag and the number of hosts initially placed in the bag. Although this method can overestimate parasitism rates due to the occurrence of superparasitism, any overestimation is likely partially nullified by instances in which hosts died prior to parasitoid emergence. That is, although multiple parasitism may have resulted in an overestimation of parasitism, there are also likely many instances in which a parasitoid attack was missed due to premature host death. For gypsy moths, it is believed that 30-50 percent of those host deaths classified as "unknown" causes may in fact result from unsubscribed parasitism (Skinner *et al.*, 1993). This bias should however be similar for both forest fragments and continuous forest, and therefore is unlikely to affect the interpretation of the results.

Estimates of mean instar

Starting in early May, sites were visited weekly to determine if host development differed between forest fragments and continuous forest. Random points were chosen within a site, and the instar of each caterpillar was recorded. A minimum of five

colonies were examined per site, or until a minimum of 100 caterpillars were found. Sampling continued each week until caterpillars reached late 4th instar, at which time dispersal of larger caterpillars seriously skewed the sampling towards the smaller instars.

For each site, mean instar was calculated for each sample period in order to determine if host phenology differed between forest fragments and continuous forest. Two sites were removed from this analysis due to the presence of virus.

Host density estimates

In this study pheromone traps were used to estimate both the background FTC density, as well as the density of FTC in individual sites after the experimental increase in density. Two traps were placed per site; one 10 m in from the forest edge, and the second 50m in from the forest edge. All traps were placed in the field prior to adult emergence, and were collected after the adult flight period. Although there was high variation even between traps from a single site, it was felt that some estimate of host density was required in order to accurately assess the true effect of landscape on parasitism.

Site characteristics

The percent canopy coverage was estimated at each site using digital photographs and ArcMap (ESRI, 2001). A total of 5 digital photos of the canopy were taken at each site; one 10m in from each corner, and one at the center of each site. ArcMap was used to contrast between black and white pixels, and an estimate of canopy cover was

then calculated by dividing the number of dark pixels (foliage) by the total number of pixels in the photo (foliage and sky). This was done for each of the five photos and averaged for the site.

Data on the abundance of *Shepherdia canadensis* (L.) Nutt. (SHEPHERDIA), the lone early season nectar source, and aspen (ASPEN), the FTC host plant, were collected during the 2nd and 3rd weeks of August. Four 50m transects were run from forest edge into the site, with each transect starting at a randomly selected point along the site edge. The number of *S. canadensis* and aspen within 1m of either side of the transect were quantified.

Statistical analysis

All mixed model analyses were done using SAS v9.1 (SAS Institute, 2005). Repeated measures mixed models and generalized linear mixed models (GLMM) were used to analyze the impacts of various landscape and demographic factors while accounting for covariance between data points caused by (1) the use of sites two years in a row, and (2) potential spatial pseudoreplication (Crawley, 2002). Where possible, a GLMM was used, because it allows proportions to be weighted by sample size, and also allows specification of a binomial error term (SAS Institute Inc., ????). The Satterwaite degrees of freedom approximation was calculated for all denomenator df in all GLMM's. Non-linear effects were assessed using the PROC GAM procedure in SAS v9.1 (SAS Institute, 2005).

The effect of fragmentation on parasitism

The impact of landscape structure on the proportion of hosts parasitized was analyzed separately for each of the three parasitoid species. In addition, I also analyzed total parasitism summed across all species to determine the impact of landscape on parasitism as experienced by FTC populations.

Landscape type (forest fragment or continuous forest, STRUCTURE) and YEAR were included as fixed factors. Both large and small scale geographic variation was accounted for by the random factors BLOCK(RESERVE) (the two different grazing reserves used in study) and STRUCTURE(BLOCK) (the spatial blocking variable pairing each forest fragment with its closest tract of continuous forest, see Fig. 2.2). STRUCTURE(BLOCK) also accounted for variation in egg mass quality, as both experimental outbreaks within a single block were made using egg masses collected from the same site in the source outbreak population. BLOCK(RESERVE) and STRUCTURE(BLOCK) were set as random factors in order to account for general habitat differences.

Although host density could potentially be thought of as a fixed factor, sites were not chosen on the basis of host density, and the experiment was not designed to evaluate the density-dependent responses of parasitoids *per se*. Therefore, host density (HOST DENSITY) at each site was in the model as a random factor.

An initial analysis showed reserve to explain little of the variation found in parasitism, and was therefore removed from further analyses. It was appropriate to remove this variable because 1) estimates of the covariance parameters for BLOCK(RESERVE) from the initial model suggest reserve effects were extremely small, 2) parasitism val-

ues from the Blackfoot reserve fell within the distribution of values from the Black Bear reserve (Fig. 2.3).

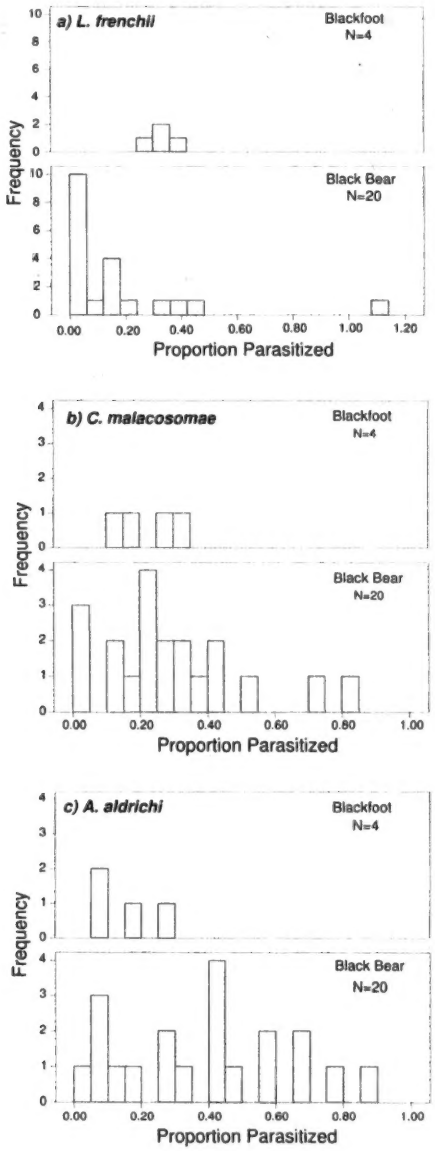

Figure 2.3: Histogram of the distribution of parasitism by a) *L. frenchii*, b) *C. malacosomae*, and c) *A. aldrichi* from both the Blackfoot and Black Bear reserves. N = the number of sites in each reserve.

Overdispersion was evident for data from all three parasitoid species (Table 2.4), suggesting that 1) fixed factors may be correlated, or 2) other unexamined factors are affecting the patterns of parasitism in this landscape (Crawley, 2002). There is no reason why STRUCTURE(BLOCK) and YEAR would be correlated since there was no change in landscape changing between years. Overdispersion was markedly reduced by accounting for location in the site (edge vs. interior).

Additional effects of isolation and patch size

Additional effects of landscape connectedness and patch size on parasitism were explored by examining the residuals from the initial analysis of the effects of structure. I chose to use the residuals for this analysis, because I was attempting to answer the the question, "Is there an additional effect of patch size, isolation distance, or connectivity on parasitism beyond the fact that fragments are disconnected from continuous forest?". By using the residuals, I removed the effect of a site being connected or not, and can therefore truly examine the effects of isolation and patch size. Only the residuals for data from forest fragments were used in this analysis since "patch" size and "isolation distance" are meaningless for continuous forest sites.

A generalized linear model (GLM) was used to analyze any linear effects of the factors examined, wheras a generalised additive model (GAM) spline was used to identify any non-linear effects of isolation or patch size on parasitism. The spline fit is a non-parametric smoother which can capture the shape of the data without any preconceived notions about the relationship between the dependent and independent variables (Crawley, 2002). The spline fit of the data was therefore done primarily as an exploratory tool. If the spline fit was significant, I examined the relationship

between parasitism and the log of the factor of interest (exponential fit), as a curve which asymptotes at some level of isolation or patch size is likely to provide the most biologically realistic non-linear response. Each of the factors was analyzed separately.

PATCH SIZE in ha was calculated from 1:40 000 (Black Bear) and 1:20 000 (Blackfoot) scale air photos. ISOLATION was the distance in meters from the edge of the patch to the nearest tract of continuous forest, with continuous forest defined as the forest which surrounds the grazing reserve. An index of the connectedness, I, (CONNECTEDNESS) (Cronin, 2003) of the landscape surrounding the fragment was calculated as:

$$I = \frac{1}{\sum_i^4 A_i e^{-D_i}} \tag{2.1}$$

where D is the distance to, and A is the area of, the nearest patch in each of four quadrants around the patch of interest. A value of 10 ha was used for A if the nearest "patch" was the continuous forest, as this value is double the size of the largest patch. Large values of I represent greater isolation and less connected landscapes.

Edge effects on parasitism and FTC development

The location in a site (edge or interior) was added to the initial GLMM analysis in order to determine if proximity to forest edge affected parasitism rates. The addition of this factor reduced the overdispersion seen in the initial analysis of the effects of fragmentation on parasitism (p. 25).

Location in the site (LOCATION) was set as a fixed factor along with STRUCTURE and YEAR. (STRUCTURE)BLOCK, LOCATION(STRUCTURE) and RE-

SERVE were set as random factors. The interaction between structure and location was included to see if edge effects were more prevalent in fragments than in continuous forest (or vice versa).

Because differences in developmental rates of caterpillars can alter the window of opportunity for parasitoid attack, thereby affecting parasitism, the effect of fragmentation on FTC development was also examined. This was done by comparing the mean instar of FTC in forest fragments to that found in continuous forest at each point in time. Mean instar was calculated as:

$$\frac{\sum_i^4 n(i)}{N} \tag{2.2}$$

where n is the number of larva collected which belonged to a specific instar, i is the instar group (ie. 1-4), and N is the total number of larvae collected.

Phenology data were collected only in 2004. A repeated measures mixed model was used for this analysis, with STRUCTURE and TIME (the 5 weeks during which mean instar was monitored) set as fixed factors, and BLOCK(RESERVE) and STRUCTURE(BLOCK) used as random factors. A significant interaction between time and structure was taken as an indication of differential host phenology between the two types, with the prediction that host phenology would be more rapid in forest fragments due to potentially higher ambient temperature.

Additional site effects

The residuals from "The effect of fragmentation on parasitism" (p. 25) were used here to further examine the effects of site characteristics; SHEPHERDIA, PERCENT

CANOPY COVER, and ASPEN. The methodology here was the same as that used to examine additional effects of patch size and isolation (p. 28).

CANOPY COVER is an estimate of the percent canopy cover in each sites. *S. canadensis* is the sole nectar source for early emerging parasitoids. ASPEN is the absolute number of aspen (the FTC host plant) in the study site, as parasitoids have been shown to be attracted to the host plant of their insect host (Mondor & Roland, 1997).

Results

A total of 942 FTC larvae and 409 FTC pupae were collected in this study. 702 parasitoid puparia were identified as belonging to the Orders Tachinidae, Sarcophagidae, and Ichneumonidae (Table 2.2). *L. frenchii* (Tachinidae) and *C. malacosomae* (Tachinidae) dominated the late larval parasitoid guild, while *A. aldrichi* (Sarcophagidae) was the dominant pupal parasitoid, parasitizing almost 40% of all pupæ collected. *L. frenchii*, *C. malacosomae*, and *A. aldrichi* were the only parasitoids sufficiently abundant to permit meaningful statistical analysis (Table 2.2), and will thus be the focus of this paper.

The composition of the parasitoid complex found here differs markedly from that typically present in FTC outbreaks (Parry, 1995; Roland & Taylor, 1997; Witter & Kulman, 1979). Two of the outbreak specialists, *L. exul* and *P. pachypyga*, were rare in this study, while the polyphagous generalist parasitoid *L. frenchii* and *C. malacosomae* were more abundant than in most studies. For more details regarding community composition, see Chapter 3.

Table 2.2: Parasitoid species identified from the Black Bear and Blackfoot reserve. Proportion of hosts parasitized was calculated as number of parasitoids collected divided by total number of larvae (or pupae) collected. Total larvae colected = 942, Total pupae collected = 409.

Species	Total # Collected	Proportion Hosts Parasitized
Tachinidae		
Lespesia frenchii	175	0.19
Carcelia malacosomae	247	0.26
Leshenaultia exul	18	0.02
Patelloa pachypyga	2	0.002
Exorista mella	41	0.04
Euexorista futilis	3	0.003
Ichneumonidae		
Agrypon anale	24	0.03
Sarchophagidae		
Arachnidomyia aldrichi	156	0.38
Pseudosarcophaga affinis	36	0.09

Effects of fragmentation on parasitism

Overall larval and pupal parasitism was not statistically different between hosts collected from forest fragments and from continuous forest, however in both cases parasitism was slightly higher in forest fragments (Fig. 2.4, Table 2.3). *L. frenchii* was the only species to show a significant response to landscape (Table 2.4), with higher parasitism in fragments (Fig. 2.4). There was no significant effect of landscape on parasitism by either *C. malacosomae* or *A. aldrichi*. There was no significant effect of year on parasitism for any of the parasitoids species examined (Table 2.4).

There were no additional linear effects of isolation distance, landscape connectedness, nor patch size on parasitism by any of the three species (Table 2.5). There was a significant non-linear effect of isolation distance on parasitism by *L. frenchii* (Table 2.5), but this was significant only for the spline fit (Fig. 2.6), not for the exponential

Table 2.3: Generalized linear mixed-effects model of overall larval and pupal parasitism in forest fragments and continuous forest. For fixed effects I provide type 3 F-statistics with associated df and P values. For random effects, I provide covariance parameters and associated standard errors.

Larval parasitism

Factor	*Co − Variance Par.*	*ndf, ddf*	*F*	P
Structure		1, 13.93	1.11	0.310
Year		1, 13.93	0.14	0.710
Year*Structure		1, 13.93	0.92	0.354
Structure(Blocks)	0			
HostDensity	0			
Dispersion parameter=1.15				

Pupal parasitism

Factor	*Co − Variance Par.*	*ndf, ddf*	*F*	P
Structure		1, 9.891	0.36	0.562
Year		1, 7.936	0.05	0.832
Year*Structure		1, 7.936	0.30	0.597
Structure(Blocks)	0.104+/-0.756			
HostDensity	0			
Dispersion parameter=0.95				

Table 2.4: Generalized linear mixed-effects model of parasitism in forest fragments and continuous forest for three FTC parasitoids. Format as in Table 2.3

L. frenchii

Factor	$Co-Variance\ Par.$	ndf, ddf	F	P
Structure		1, 10.30	5.63	0.039
Year		1, 11.26	0.00	0.969
Year*Structure		1, 11.26	1.23	0.291
Structure(Blocks)	0.684+/- 0.464			
HostDensity	0			
Dispersion parameter=2.17				

C. malacosomae

Factor	$Co-Variance\ Par.$	ndf, ddf	F	P
Structure		1, 20.00	0.16	0.689
Year		1, 20.00	0.18	0.674
Year*Structure		1, 20.00	0.00	0.962
Structure(Blocks)	0			
HostDensity	0			
Dispersion parameter=5.28				

A. aldrichi

Factor	$Co-Variance\ Par.$	ndf, ddf	F	P
Structure		1, 10.66	0.00	0.968
Year		1, 10.26	0.11	0.746
Year*Structure		1, 10.26	0.70	0.423
Structure(Blocks)	0.990+/-0.708			
HostDensity	0			
Dispersion parameter=2.17.				

fit.

Table 2.5: Coefficient and the associated significance of the linear, non-linear spline, and exponential fit of the effect of patch size, isolation, and connectedness on parasitism by three species of FTC parasitoids.

L. frenchii

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
Patch Size	-0.00002(0.427)	0.069	-1.11(0.471)
Isolation Distance	0.00002(0.774)	0.040	0.721(0.684)
Connectedness	0.138(0.284)	0.420	

C. malacosomae

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
Patch Size	-0.000003(0.918)	0.527	
Isolation Distance	0.00039(0.697)	0.527	
Connectedness	0.054(0.693)	0.667	

A. aldrichi

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
Patch Size	0.00003(0.913)	0.781	
Isolation Distance	-0.0005(0.492)	0.888	
Connectedness	-0.086(0.449)	0.919	

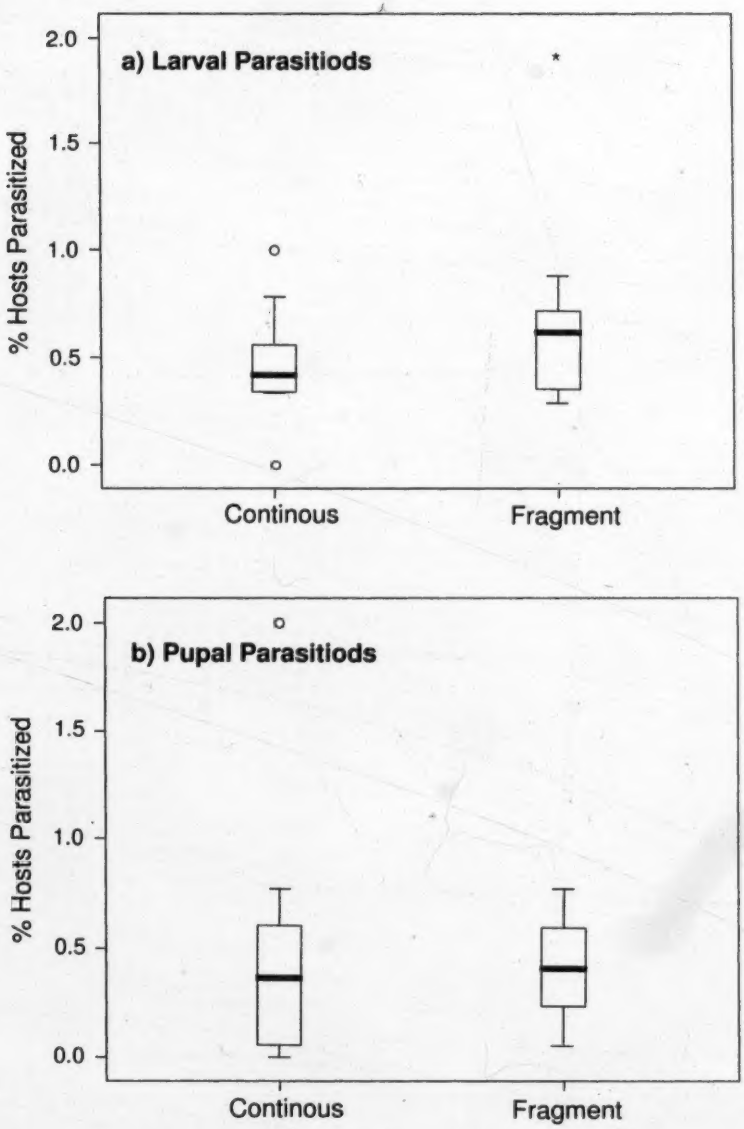

Figure 2.4: The effect of landscape structure on the proportion of forest tent caterpillar parasitized by a) late larval and b) pupal parasitoids. The dark line represents the median, with the surrounding box showing the interquartile range. Whiskers show range of all values which are not classified as outliers. o = outliers in 1.5-3.0 box lengths from upper or lower edge of box. * = points which are greater than 3 box lengths from upper or lower edge of box.

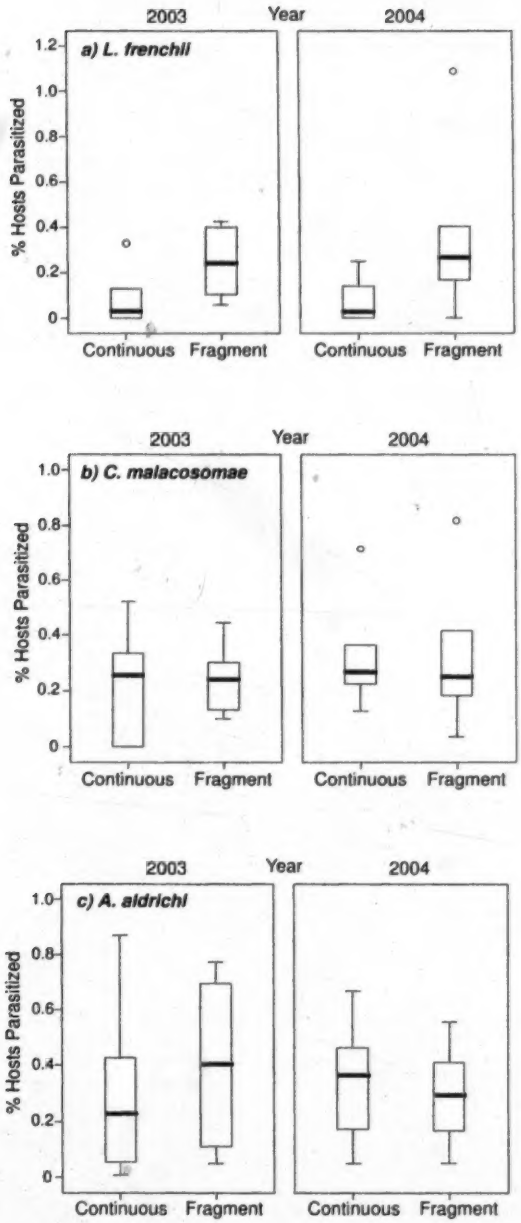

Figure 2.5: The effect of landscape structure on the proportion of hosts parasitized by a) *L. frenchii*, b) *C. malacosomae*, and c) *A. aldrichi* in both 2003 and 2004. Plot as in Fig 2.4

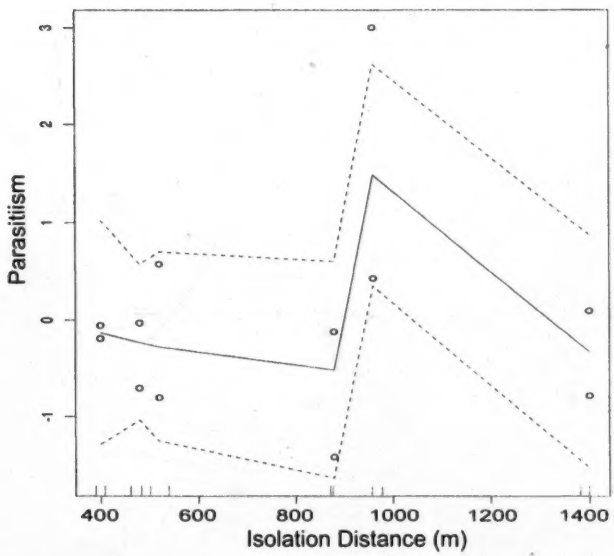

Figure 2.6: Spline fit of the effects of isolation distance on parasitism by *L. frenchii*. Dotted line shows standard error.

Edge effects on parasitism and host development

Only *C. malacosomae* showed a marginally significant (P=0.086) response to location within the site (Table 2), with higher rates of parasitism at the forest edge (Fig. 2.7). There was no interaction between structure and location for any of the three species, suggesting the absence of edge effects was similar for both forest fragments and continuous forest (Table 2.6). The overdispersion seen in main analysis of landscape was reduced with the addition of location within a site, as the dispersion parameters for this analysis were close to one for all species.

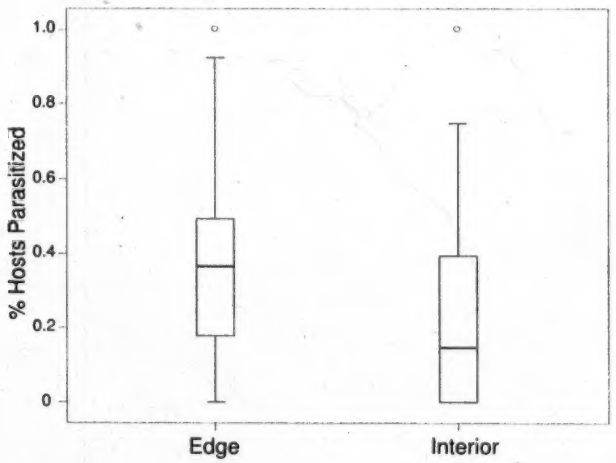

Figure 2.7: Parasitism by *C. malacosomae* at the edge and interior of forest stands. Plot as in Fig. 2.4

Table 2.6: Generalized linear mixed-effects model of the effects of proximity to forest edge and of forest structure on parasitism by three FTC parasitoids. Format as in Table 2.3

L. frenchii

Factor	*Co − Variance Par.*	*ndf, ddf*	*F*	P
Structure		1, 17.40	4.22	0.055
Year		1, 18.22	0.05	0.824
Location		1, 17.73	2.04	0.172
Structure*Location		1, 17.74	0.78	0.389
Year*Location		1, 18.22	0.10	0.755
Structure(Block)	0.675+/-0.604			
Location(Structure)	0.288+/- 0			
Dispersion parameter = 0.91				

C. malacosomae

Factor	*Co − Variance Par.*	*ndf, ddf*	*F*	P
Structure		1, 18.29	0.37	0.550
Year		1, 19.89	0.39	0.541
Location		1, 18.26	3.30	0.086
Structure*Location		1, 18.29	0.06	0.817
Year*Location		1, 19.89	1.68	0.209
Structure(Block)	0.076+/-0.396			
Location(Structure)	0.045+/- 0			
Dispersion parameter = 1.05				

A. aldrichi

Factor	*Co − Variance Par.*	*ndf, ddf*	*F*	P
Structure		1, 16.78	0.16	0.692
Year		1, 7.951	0.00	0.976
Location		1, 16.87	0.02	0.890
Structure*Location		1, 16.78	0.19	0.667
Year*Location		1, 7.951	0.11	0.749
Structure(Block)	1.681+/-1.240			
Location(Structure)	0.640+/- 0			
Dispersion parameter=1.00				

There was no significant STRUCTURE by TIME interaction on mean instar (Table 2.7), suggesting that host development rate was similar in both fragments and continuous forest. The window of opportunity for parasitism attack is therefore sim-

ilar in both forest fragments and continuous forest.

Table 2.7: Repeated measures mixed-effects model of FTC maturation rate in forest fragments and continuous forest. Format as in Table 2.3

Factor	$Co-Variance\ Par.$	ndf, ddf	F	P
Structure		1, 10	0.17	0.693
Time		1, 36	160.11	0.0001
Structure*Time		4, 36	1.03	0.403
Reserve	0.014			
Block(Reserve)	0.001			
Structure(Block)	0.002			

The effect of site characteristics on parasitism

Fine scale variation in plant community structure has little effect on parasitism by either *C. malacosomae* or *A. aldrichi*, as there was no effect of *S. canadensis*, tree canopy cover, or the number of aspen on parasitism by either of these species (Table 2.8). *L. frenchii* showed a significant non-linear response to *S. canadensis* (Fig. 2.8). However the exponential fit was non-significant (Table 2.8).

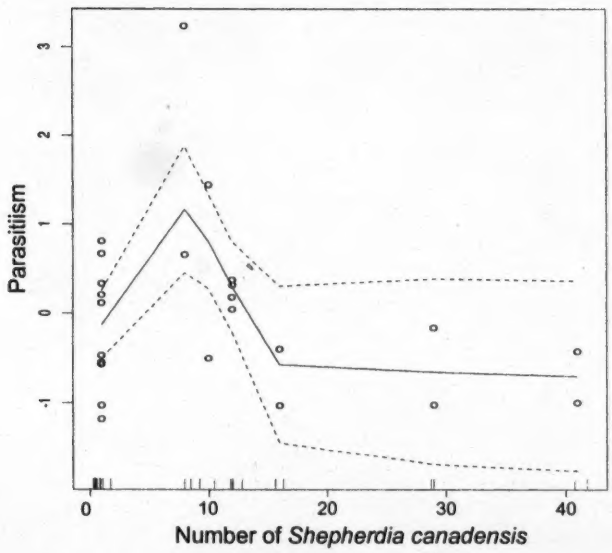

Figure 2.8: Spline fit of the effect of *Shepherdia canadensis* abundance on parasitism by *L. frenchii*. Dotted line shows standard error.

Table 2.8: Coefficient and the associated significance of the linear, non-linear spline, and exponential fit of the effect of abundance of *S. canadensis*, percent canopy cover, and abundance of aspen on parasitism by three species of FTC parasitoids.

L. frenchii

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
S. canadensis	-0.018(0.260)	0.004	-0.035(0.915)
% Cover	2.968(0.140)	0.136	
Aspen	0.002(0.560)	0.213	

C. malacosomae

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
S. canadensis	-0.012(0.544)	0.159	
% Cover	1.769(0.434)	0.585	
Aspen	-0.001(0.389)	0.342	

A. aldrichi

	Linear	***spline***	***Exponential***
Factor	Coefficient(P)	P	Coefficient(P)
S. canadensis	0.010(0.575)	0.369	
% Cover	1.536(0.522)	0.510	
Aspen	-0.002(0.354)	0.606	

Discussion

Forest fragmentation is believed to negatively impact parasitoid movement, thereby affecting the dynamics of the FTC host-parasitoid systems (Roland, 1993, 2000; Roland & Taylor, 1997). The results of this study refute this hypothesis, however, and suggest that parasitoid movement is not impacted by forest fragmentation at this scale. Parasitism by *C. malacosomae* and *A. aldrichi* did not differ significantly between connected and disconnected forest fragments, and for *L. frenchii* was greater in forest fragments. Furthermore, there was no effect of isolation distance, landscape connectedness, or patch size on parasitism by any of the species examined. There are several potential explanations for this pattern. Firstly, the movement of parasitoids may in fact not be inhibited by forest clearings. This suggests that the reduced parasitism seen in fragmented forests (Roland, 2000; Roland & Taylor, 1997) may be caused by factors not related to parasitoid movement between forest patches. Secondly, higher parasitism exhibited by *L. frenchii* in forest fragments may result from differences in the frequency of superparasitism between forest fragments and continuous forest. Thirdly, the distribution of parasitoids, and hence parasitism, may reflect the distribution of other factors such as plant community, or alternative hosts. Finally, I may not have truly measured the parasitoid response to landscape due to low statistical power, and an inability to create a strong point source to which parasitoids can respond.

Despite the importance of insect movement in a variety of ecological processes (pollination, predation, nectar feeding, parasitism, etc), there has been little work on the direct effect of landscape on insect movement. This is due to the inherent

difficulty of working with small organisms at large spatial scales. Because of this, there is only limited information on the actual dispersal capabilities of many insect species, much of which is gained indirectly. In host parasitoid systems, movement can be indirectly examined by looking at patterns of parasitism in the landscape. For example, if parasitism is lower in isolated forest fragments, we could infer that parasitoids are unable to move through the surrounding matrix with the same efficiency as through forested habitat. This type of pattern has been observed empirically in several studies. The parasitoid community of herbivores feeding on red clover was reduced by 19-60% in isolated sites compared to parasitism in non-isolated habitat (Kruess & Tscharntke, 1994). Similarly, the parasitoids of seed feeding insects are affected more by isolation than were their herbivorous hosts, with parasitism reduced significantly by a couple of hundred metres of isolation (Kruess & Tscharntke, 2000). Other insects however, are particularly vagile, and may therefore not be affected by such small scale fragmentation (Tscharntke & Roland, 2002). For example, the minute fairyfly egg parasitoid (Hymenoptera) colonized host patches isolated by up to 1km (Cronin & Strong, 1999). There can also be variation between parasitoids within a single host-parasitoid community, as many host populations of the butterfly *Melitaea cinxia* (Linnaeus) were inaccessible to the parasitoid *Cotesia melitaearum* (Wilkinson) because of its limited dispersal ability, whereas other parasitoids were able to access all groups of hosts (Van Nouhuys & Hanski, 2002). Although there has been very little work done on the dispersal abilities of FTC parasitoids, the large pupal parasitoid *A. aldrichi* is believed to disperses upwards of 400m when colonizing isolated habitat patches (Roland, unpublished data), while smaller parasitoids in this system are successful at shorter distances (Roland & Taylor, 1997). The response

of parasitoids to fragmentation is therefore species-specific (Roland & Taylor, 1997; Van Nouhuys & Hanski, 2002), and dependent on the ability of individual species to move through the landscape.

The FTC parasitoids examined here were not inhibited by the isolation distances used in this study, as all of the species examined were found in isolated patches. Furthermore, parasitism did not differ between forest fragments and continuous forest for overall larval or pupal parasitism. Although *A. aldrichi* may be unaffected by fragmentation at this scale, due to its large size and efficient dispersal ability, I was surprised to find that neither *L. frenchii*, nor *C. malacosomae* (two of the smallest parasitoids in this system) were affected by the isolation distances used here. Initially, I felt that this landscape effect may have resulted from isolation distances not being a true measure of the isolation experienced by the parasitoids; that the landscape was more connected than the simple isolation distance would suggest. Although many forest fragments were quite isolated from continuous forest, they were potentially connected through a chain of suitable habitat patches through which parasitoids could disperse. The non-significant effect of landscape connectedness (Table 2.5) indicated that parasitoids may not be using the surrounding habitat patches as "stepping stones". This non-effect of both patch isolation and connectedness on parasitism suggests that FTC parasitoids are able to move through the open grasslands of the fragmented landscape and indicates that reduced parasitoid movement between forest patches is not the mechanism responsible for low parasitism in fragmented forests as observed in previous studies (Roland, 2000; Roland & Taylor, 1997).

The higher parasitism exhibited by *L. frenchii* in isolated fragments may at first appear counter intuitive, although the pattern is not unique to this study. Parasitism

by the the braconid (*Aleiodes* n. sp) was higher in small, isolated patches (Doak, 2000), although tachinids in that study showed no such pattern. Similar results have been found in the FTC host-parasitoid system, as both the braconid *Aleiodes malacosomatos* (Mason) (Roland, 2000) and the tachinid *C. malacosomae* (Roland & Taylor, 1997) exhibited higher parasitism in fragmented forests. Elevated parasitism in isolated patches may result from parasitoids following an optimal foraging strategy, whereby search time and oviposition effort are determined by the time or energy invested in traveling to that patch. This has been supported empirically for some species, as fairyfly egg parasitoids increase their oviposition effort as dispersal distances increased (Cronin & Strong, 1999). Doak (2000) suggested that similar processes may be acting on braconid and ichneumonid parasitic wasps attacking *Itame andersoni* (Swett.) (Geometridae) given that parasitism was highest in isolated patches. If *L. frenchii* was following this type of search strategy, we would expect parasitism to increase with isolation. Despite higher parasitism in disconnected forest patches, I found no positive additional effect of isolation on *L. frenchii* parasitism rates. It is therefore likely that something about the nature of disconnected forest fragments, regardless of their spatial arrangement in the landscape causes elevated parasitism. Both *L. frenchii* and *C. malacosomae* can have multiple larvae emerge from a single host (Williams *et al.*, 1996). However, because of limitations in rearing, I could not determine how often this occurred, and have likely overestimated the true parasitism rates of these species. Higher parasitism in fragments could occur if parasitoids if parasitoids are less likely to leave a forest fragment than they are an equivalent area of continuous forest, because of negative responses to the forest edge. Such behavior could lead to repeated encounters with previously attacked host

colonies, resulting in elevated parasitism, and an increase in the frequency of superparasitism. Responses to habitat boundaries have been seen in other insect species, as Fenders blue butterflies (*Icaricaia icarioides fenderi* (Macy)) exhibit altered behavior within 10-22 m of habitat boundaries (Schultz & Crone, 2001), while the bog fritillary butterfly (*Proclossiana eunomia* (Esper)) engaged in U turns 40% more often when reaching the habitat edge than they did in continuous landscapes (Schtickzelle & Baguette, 2003). This trait is not unique to Lepidoptera, as hoverfly movement is restricted by poplar boundaries in agricultural landscapes (Wratten *et al.*, 2003a). Furthermore, the strength of the insect response to boundaries may depend on the degree to which habitats on either side of the boundary differ. Soft boundaries (similar habitat on either side of the boundary) are more permeable to movement than are "hard" boundaries (dissimilar habitat on either side of boundary) (Stamps *et al.*, 1987), although few studies have shown this empirically (Collinge & Palmer, 2002). The boundary contrast in my study area is hard, as the transition from forest to grassland is abrupt. If FTC parasitoid emigration from forest fragments is inhibited by a negative response to forest edge, parasitoids may have repeated encounters with host colonies (Roland, 2000). If such a mechanism is operating here, the observed parasitism rates may reflect both an increase in the actual parasitism rate experiences by host larvae, as well as an increase in the frequency of multiple parasitism events between the two landscape types.

Despite the above caveat, there are certain facts that indicate that parasitoids remain in forest fragments. If the elevated parasitism by *L. frenchii* in disconnected forest patches is caused by constrained movement at the boundary contrast, we may expect parasitoids to pool in edge habitat, resulting in elevated parasitism. No such

response, however, was seen in this study. We may also expect *L. frenchii* parasitism to be greatest in smallest fragments due to the smaller area over which they would have to search. Yet there was no significant effect of patch size on *L. frenchii* parasitism. This does not necessarily refute the hypothesis of reduced movement out of a patch, as detection of these subtle responses to forest edge may require direct observation of parasitoid movement. The potential inhibitory effects of patch boundaries on parasitoid emigration from a patch may appear contradictory given the apparent ability of parasitoids to colonize isolated forest fragments. This could, however, simply exemplify the difference between the response of insects to habitat cues during foraging, and long distance active dispersal between habitat patches. That is, habitat cues which may typically arrest insect activity during "trivial" movement, may not operate when the insect is traveling between habitat patches (Kennedy, 1975). If this is the case, parasitoids may be inhibited by forest edge when foraging for hosts, but not so when actively dispersing long distances between suitable habitat. Planktonic, or passive dispersal, of small parasitoids (such as egg parasitoids) on wind currents could also result in parasitoids passively entering a patch. However, we would expect to see a negative relationship between isolation and parasitism if this were the case.

Although parasitism by *L. frenchii* was not affected by forest edge, *C. malacosomae* did show a marginally significant response to location within a patch, with higher parasitism near forest edge (p=0.085) (Figure 2.7). This could result from differing micro-climate found in edge habitat (Landis & Haas, 1992; Murcia, 1995; Saunders *et al.*, 1991), or from this species exhibiting the previously described negative response to patch boundaries. This higher parasitism in edge habitat may explain the positive response of this species to forest fragmentation (Roland & Taylor, 1997), as

the higher parasitism exhibited by this species in fragmented landscapes may result from its ability to exert greater mortality on forest edge.

The ability of FTC parasitoids to move through the fragmented forest implies that parasitoids are not restricted to certain areas of the landscape, and that parasitism should reflect other factors, such as habitat quality rather than fragmentation. The presence of nectar sources, on which parasitoids rely for energy (Casas *et al.*, 2003) and for egg maturation (Berndt & Wratten, 2005) may be particularly important in determining parasitoid distribution. Both theoretical (Russell, 1989) and empirical (Landis & Haas, 1992; Thies *et al.*, 2003) work suggest that parasitoids may be more effective at controlling herbivores in complex habitats in part because of the presence of nectar sources. Parasitoids can aggregate in areas with abundant nectar sources, resulting in elevated parasitism in these areas (for review see Wratten *et al.*, 2003b). In my system, *S. canadensis* is the lone nectar source present when early season parasitoids such as *A. aldrichi*, *L. exul*, and *P. pachypyga* emerge. However none of the three parasitoids examined here showed a significant response to this nectar source. *L. frenchii* and *C. malacosomae*'s non-responses to *S. canadensis* are likely due to their emergence later in the season when other nectar sources are present. I suspect that *A. aldrichi* may respond to this nectar source, but does so on a larger spatial scale than that measured here. Although parasitoids require a spatial co-ocurrence of both hosts and nectar (Jervis *et al.*, 1993), it is unlikely that *A. aldrichi* would require both to be present in a small area given its dispersal capabilities. In order to accurately gauge the relationship between the distribution of *S. canadensis* and parasitism, a larger scale measurement of the distribution and abundance of this plant is needed.

Parasitoids may also respond to other site characteristics that signal suitable FTC habitat. For example, parasitoids can respond to the larval host plant. The hymenoptera parasitoid *Diaeretiella rapae* (McIntosh) uses volatile mustard oils in order to find cruciferous plants on which its host feeds (Read *et al.*, 1970). Parasitism could also be affected by the openness of the canopy in a site, as areas with open canopies may have higher ambient temperature, which could affect developmental processes both of hosts (Hodson, 1941), and of parasitoids (Ichiki *et al.*, 2003). This could alter the window of opportunity for parasitoid attack. However, there was no effect of the number of aspen, or canopy cover on parasitism by any of the species examined, suggesting that these habitat characteristics, measured at this scale, do not have a strong effect on parasitism. Thus, although habitat is important for many invertebrate natural enemies (Kruess, 2003; Russell, 1989), it appears to have little effect on parasitism in this system. This study was not designed to examine parasitoid habitat preference however, and as such, these three measures (*S. canadensis* abundance, canopy cover, and aspen abundance) do not effectively characterize my sites. A more detailed analysis of the FTC parasitoid response to habitat is therefore needed in order to truly understand the relationship between habitat and parasitism.

The limited effect of both landscape and habitat in this study suggest that other factors may be more important in determining parasitism. I believe that the life history characteristics that allow *L. frenchii*, *C. malacosomae*, and *A. aldrichi* to thrive when host densities are low, may determine their distribution. For example, the abundance of polyphagous parasitoids may be greater in those sites with multiple host species (Stireman & Singer, 2002). *L. frenchii* is particularly polyphagous, having been reared from almost 50 other Lepidoptera species (Schmidt, 2001), and by having

two generations per year, only one of which uses FTC as a potential host (Williams *et al.*, 1996). Because of this, *L. frenchii*'s parasitism is likely strongly linked to the distribution of its alternate hosts on which its second generation relies (Parry, 1995). Although the majority of Lepidoptera species in Alberta are negatively affected by forest fragmentation (Schmidt, 2001), *L. frenchii*'s higher parasitism in forest fragments could occur if its alternate hosts (those on which its second generation rely) are more prevalent in open landscape. Neither *C. malacosomae*, nor *A. aldrichi*, are as polyphagous as *L. frenchii*, but both have been reared out of alternative host species (Table 3.1). Like *L. frenchii*, *C. malacosomae* also superparasitize hosts, which may be an adaptation for survival during the endemic phases of the host cycle (Parry, 1995). *A. aldrichi* on the other hand, has characteristics of both a specialist parasitoid and a scavenger (Hodson, 1939). Scavenging would allow this species to survive in areas with low FTC densities.

The role of parasitoids in regulating endemic host populations of otherwise cyclic defoliators is not well studied (but see Mills, 1990, and Skinner, 1993). However parasitoids and generalist predators were able to suppress my experimentally elevated host populations. High early-instar mortality caused by carabid beetles, birds, and Hempiteran bugs, coupled with mortality caused by parasitoids, resulted in no discernible increase in host density across years. Similar responses to experimentally elevated host density have been seen for gypsy moth (Gould *et al.*, 1990). These patterns suggest that generalist predators and parasitoids can play an important role in maintaining endemic populations of cyclic defoliators, supporting the idea of an outbreak threshold suggested by Parry *et al.* (1997). It should be noted that despite no visual increase in FTC density, pheromone trap data indicates that host densities

did increase from 2003 to 2004 in the Black Bear Grazing Reserve, but this pattern was apparent on a much larger scale (Roland, unpublished). Given this, parasitism did not differ significantly between years, suggesting that parasitoids did not increase numerically within sites. The increase in host density as seen in the pheromone trap data is likely not caused by my experimental elevation of host density. Instead, it is part of a large scale increase in host density occurring in the region, indicative of the beginnings of a new host outbreak.

The limited effect of fragmentation on parasitism seen here does not eliminate the possibility that fragmentation does impact parasitoid movement. Low sample size and limited replication are an inherent difficulty of doing large scale landscape studies at low host density. Because of this, I may lack the statistical power necessary to detect the effect of fragmentation on parasitism. Furthermore, the contrast in densities between my patches of elevated host density, and that of background densities, may have been insufficient to elicit parasitoid movement from continuous forest to forest fragments. Parasitoids can respond to, and exert significant mortality on, locally elevated populations of gypsy moth (Elkinton *et al.*, 1990; Liebhold & Elkinton, 1989), western tussok moth (Umbanhowar *et al.*, 2003), and forest tent caterpillar (Parry, 1994). However, the strength of such a response is dependent on the contrast between the areas of high host density and background densities, and on the distance to sources of parasitoids (Elkinton *et al.*, 1990). Although experimental elevations of host density can result in artificial density gradients, and hence elevated parasitism rates (Liebhold *et al.*, 2000), I believe my study suffered from the opposite problem. Hatch in my study sites was generally poor (see above), as was larval survival, resulting in host densities in my experimental sites being insufficient to create

noticeable defoliation. Caterpillar density was, at best, responsible for light defoliation based on the criteria of Hodson (1977). This is problematic as the abundance of the cues used by parasitoids to find host populations, such as plant compounds released on defoliation, host frass, or combinations of the two (Mondor & Roland, 1997, 1998), are strongly dependent on caterpillar density. An accurate test of my hypothesis regarding the inhibitory impacts of fragmentation on parasitoid movement implicitly requires the presence of a strong point source or cue to which parasitoids can move. Although the FTC densities in my sites were undoubtedly higher than the background densities, I believe the limited defoliation created by these populations may have provided insufficient cues to draw parasitoids from outside the patch. Furthermore, those FTC parasitoids which have been shown to exhibit density dependent responses (*P. pachypyga*, *A. malacosomatoes* (Parry *et al.*, 1997)) were extremely rare in my study area, and were not part of the statistical analysis.

Despite the before mentioned limitations, I believe that the results of this study provide evidence that forest clearings do not reduce the ability of certain FTC parasitoids to colonize isolated forest patches. All of the major FTC parasitoid species were found in disconnected habitat, and parasitism was not lower in forest fragments for any of the species examined. This does not mean, however, that parasitoid foraging behavior is not affected by fragmentation, as foraging and dispersal between habitat patches are two unique processes (Kennedy, 1975). The negative effect of large scale fragmentation observed for the majority of FTC parasitoids during FTC outbreaks (Roland & Taylor, 1997) may therefore not result from inhibited parasitoid movement between patches, but may instead be caused by more subtle parasitoid responses to factors such as increases in the amount of forest edge, or changes in habitat

quality. These subtle impacts of fragmentation, however, may be difficult to detect even with high statistical power because of the many stochastic factors that impact the system. Furthermore, the importance of finding suitable hosts (FTC or otherwise) during the endemic stage of the host cycle may play a more important role in determining the distribution of parasitoids than does landscape.

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Chapter 3

The effect of landscape and host density on the late larval parasitoid assemblage of the forest tent caterpillar (*Malacosoma disstria*)

Introduction

Parasitoids are an incredibly diverse group of insects, potentially accounting for almost 20% of all insect species (Godfray, 1994). Most insect herbivores have a complex of parasitoid species that exert a significant, and potentially regulatory role on host populations. The size, and diversity, of these parasitoid "complexes" differ among host species, ranging between 0-100 species per host species (Hochberg & Hawkins, 1993). Although the diversity of parasitoid assemblages has been linked to their ability to impact host dynamics, the findings on this topic are varied. While the number of species within a parasitoid complex can be closely correlated to both host abundance and patterns of parasitism (Kruess & Tscharntke, 1994), as well as to the ability of parasitoid complexes to control host populations (Hawkins & Gross, 1992), others have found that the ability of parasitoid assemblages to regulate host populations is not necessarily improved with higher diversity (Rodriguez & Hawkins, 2000; Tscharntke, 1992). In the case of biocontrol, the introduction of multiple parasitoid species does not necessarily result in more effective control of host populations than does the introduction of a single parasitoid species (Denoth *et al.*, 2002). Despite variation in the effect of parasitoid diversity on regulatory ability, understanding the factors which determine the makeup of parasitoid asssemblages is of interest to both insect ecologists and biocontrol practitioners, as even subtle changes in the rates of parasitism experienced by hosts, or the timing of the parasitoid attack, could alter the dynamics of the system (Wilson *et al.*, 1996). However, despite studies examining the effect of ecological factors on exophytic parasitoid communities over evolutionary time scales (Hawkins, 1988; Stireman & Singer, 2003), there has been very little research

conducted on how the makeup of parasitoid communities for a single host is affected by ecological factors over shorter time periods. For example, how do landscape factors such as forest fragmentation, or biological factors such as host dynamics, affect the structure of parasitoid communities over several generations?

Understanding how landscape and host density interact to affect parasitoid communities is of particular interest with respect to the host-parasitoid systems of cyclic defoliators, because of the role parasitoids may have in defining the duration and frequency of economically damaging host outbreaks. The parasitoid communities of cyclic defoliators are often particularly diverse because of the high degree of niche separation afforded insects in forest communities, resulting in a higher number of specialist parasitoids (Mills, 1990). The parasitoid complexes of cyclic forest defoliators may, however, also show greater temporal variation than do those of non-outbreaking forest insects because of the large changes in host density. Parasitoid communities from high and low density host populations are known to differ for a variety of host species, with one or two key species typically present at only high, or low, host densities (Mills, 1990). For example, the tachinid *Ceranthia samarensis* (Villeneuva) can dominate low density gypsy moth (*Lymantria dispar* (Linnaeus)) populations (Mills, 1990), while decreasing in importance during outbreaks when parasitoids such as *Blepharipa pratensis* (Meigan) and *Parasetigena silverstris* (Robineau-Desvoidy) are more prevalent (Fuester *et al.*, 1983). Similarly, Hoch *et al.* (2001) found that the parasitoid complexes of gypsy moth in Austria and Slovakia differed between high and low density host populations, with those parasitoids showing high parasitism in low density host populations having a reduced impact in outbreak populations. Such patterns are also present in the parasitoid complexes of spruce budworm (*Choris-*

toneura fumiferana (Clem)) (Miler & Renault, 1976), and winter moth (*Operophtera brumata* (Linnaeus)) (Embree, 1966). Outbreaks of the forest tent caterpillar (*Malacosoma disstria* Hübner) are characterized by a high abundance of specialist parasitoids (*Leschenaultia exul* (Townsend) and *Patelloa pachypyga* (Aldrich and Webber)), while generalist parasitoids have a greater relative impact at low host densities (Parry, 1995; Parry *et al.*, 1997; Williams *et al.*, 1996; Witter & Kulman, 1979). Generalist parasitoids are likely able to survive in low density host populations because their broader host range buffers them against fluctuations of any one host species (Latto & Hassell, 1988). There is a notable absence of research on factors affecting parasitoid communities in "endemic" (low density) host populations due to the logistical difficulty in sampling sparse host populations. An understanding of parasitoid complexes found in low density host populations may, however, allow for the use of endemic parasitoids as biological control agents in order to prolong the endemic phase and to decrease the frequency of host outbreaks (Mills, 1990).

Landscape is also likely to have an impact on the nature of parasitoid complexes, as theory predicts that parasitoids should be particularly susceptible to fragmentation because of the high trophic level which they occupy (Davies *et al.*, 2000; Kruess & Tscharntke, 2000; Steffan-Dewenter, 2003; Thies *et al.*, 2003). Patterns of parasitism suggest that parasitoids are responsive to landscape features such as patch size and patch isolation (Cronin, 2003b, 2004; Doak, 2000; Kruess, 2003; Kruess & Tscharntke, 2000), landscape complexity (Liebhold *et al.*, 2000; Menalled *et al.*, 1999; Tscharntke, 2000), as well as to the surrounding matrix (Cronin, 2003a). As fragmentation increases, the remaining habitat will become smaller and more isolated, which may have detrimental effects on parasitoid communities through decreased colonization success

and a reduction in parasitism in isolated patches. This pattern has been observed for parasitoids of seed-feeding insects (Kruess & Tscharntke, 2000), and for planthopper parasitoids (Cronin, 2004). Similarly, van Nouhuys & Hanski (2002) showed that many host populations of the butterfly *Melitaea cinxia* (Linnaeus) were inaccessible to the parasitoid *Cotesia melitaearum* (Wilkinson) because of its limited dispersal ability, whereas other parasitoids were able to access all groups of hosts. Such differences in parasitoid responses to isolation may result in parasitoid communities being less diverse in isolated forest fragments (e.g. Kruess & Tscharntke, 1994). Patch size may also affect parasitoid distribution within the landscape; the diversity of parasitoid communities of the herbivores of *Vicia sepium* L. was greatest in both the largest and smallest patches, and species composition differed dramatically between the two (Kruess & Tscharntke, 2000). Furthermore, rare parasitoids are expected to have a higher susceptibility to stochastic extinction in small forest patches because of their low abundance (Connor & McCoy, 1979; Davies *et al.*, 2000).

Forest tent caterpillar parasitoids respond to forest fragmentation in a size-dependent fashion, with smaller parasitoids showing the strongest response to fragmentation measured at small spatial scales, while large parasitoids respond to landscape at larger spatial scales (Roland & Taylor, 1997). Furthermore, the strength and direction of the parasitoid response to fragmentation can differ among parasitoid species. For example, *Carcelia malacosomae* Sellers inflicted higher parasitism in fragmented forests, while all other parasitoids in the system responded negatively to forest fragmentation (Roland & Taylor, 1997). Variation in the nature of the parasitoid response to landscape could translate into differential parasitoid community structure within fragmented forest compared to continuous forest. Such community changes

may result in host populations experiencing differing levels of mortality depending upon the degree of forest fragmentation within the landscape, subsequently altering host-parasitoid dynamics (Davies *et al.*, 2000; Maron & Harrison, 1997; Roland, 2005; Thies *et al.*, 2003) and resulting in more frequent, or longer lasting, outbreaks in more fragmented forest (Roland, 1993).

Furthermore, the impact of fragmentation may vary with host abundance since the composition of parasitoid species complexes can differ between high and low density host populations. Such an interaction has not been previously examined; most studies of the effects of landscape do so only during host outbreaks. In order to fully understand the relationship between landscape and the host-parasitoid system of cyclic defoliators, we must examine whether an interaction exists between these two factors. That is, does forest fragmentation affect the parasitoid complex more, or less, during host outbreaks compared to during the endemic phase of the host cycle?

The larval parasitoid complex of FTC is dominated by a core group of tachinid flies found in most host populations across the prairies and boreal forests of North America; *L. exul*, *P. pachypyga*, *Lespesia frenchii* (Williston) and *C. malacosomae* (Parry, 1995; Parry *et al.*, 1997; Roland, 1993; Roland & Taylor, 1997; Witter & Kulman, 1979). Within the FTC parasitoid community, host specificity ranges from the extremely polyphagous *L. frenchii* (50 alternative hosts), to *L. exul* and *P. pachypyga*, with 2 and 3 host species respectively (Schmidt, 2001). Species within the FTC late larval parasitoid complex also differ with respect to the cues to which they respond while searching for hosts (Mondor & Roland, 1997, 1998), as well as in their mode of attack (Table 3.1). Those species known to increase numerically in response to elevated host density (*P. pachypyga, L. exul*) are more likely to be prevalent during FTC

outbreaks, while generalist parasitoids such *L. frenchii* and *Exorista mella* (Walker) which are able to survive on alternative host species may be better able to persist in areas where FTC are scarce (Parry, 1995; Schmidt, 2001; Williams *et al.*, 1996; Witter & Kulman, 1979). It should be noted that the distribution of those parasitoid species with two generations per year (*L. frenchii*, *E. mella*), and *Euxorista futilis* (Osten Sacken) (Williams *et al.*, 1996) may be particularly variable because of their dependency on alternate hosts for survival of the second generation.

In this study, I attempt to evaluate how both landscape and host density affect the relative abundance of tachinid species in the FTC late larval parasitoid community. I examine how the response of parasitoid assemblages to forest fragmentation differs in outbreaking and endemic host populations. I hypothesize that parasitoid assemblages present during host outbreaks will have a larger proportion of specialist parasitoids than do endemic populations, whereas generalist parasitoids dominate in low density host populations (relative to their specialist counterparts) due to their ability to utilize alternative hosts (Latto & Hassell, 1988; Schmidt, 2001). I predict that parasitoid communities differ between highly fragmented forest and continuous forest, with patterns consistent with the findings of Roland & Taylor (1997); that the smaller parasitoid *C. malacosomae* is expected to thrive in fragmented forest, while *L. exul* and *P. pachypyga* are affected negatively by forest fragmentation. Finally, since specialist parasitoids are believed to be affected more by forest fragmentation than are generalist parasitoids, because of fine grained habitat requirements which may not be met in small patches (Tscharntke *et al.*, 2002), I believe that parasitoid complexes from outbreaking FTC populations will respond more strongly to fragmentation than will those from endemic host populations.

Table 3.1: Members of the forest tent caterpillar late larval tachinid parasitoid community. The "Instar of emergence" refers to the instar from which the parasitoid leaves the host. "Mode of parasitism" refers to whether parasitoids lay eggs directly on hosts, or on the surrounding foliage (for host ingestion). "Phase specialty" refers to the phase of the host cycle during which that species was most prominent with respect to abundance and percent parasitism

Species	Instar of emergence[abf]	Mode of parasitism	# of alternative hosts[b]	Phase specialist	# of Generations per year [e]
C. malacosomae	5th/early pupa	larva[ae]	8	endemic[a]	1
L. frenchii	5th/early pupa	larva[e]	48	declining[a], endemic[af]	2
P. pachypyga	5th/early pupa	foliage[ae]	3	outbreak[ade]	1
L. exul	5th	foliage[ae]	2	outbreak[adf]	1
E. mella	n/a	larva[e]	43	n/a	2
E. futilis	n/a	foliage[e]	19	n/a	2

[a] (Parry, 1995)
[b] (Roland & Taylor, 1997)
[c] (Schmidt, 2001)
[d] (Sippel, 1962)
[e] (Williams *et al.*, 1996)
[f] (Witter & Kulman, 1979)

Methods

Collection methods and rearing

Only data for the late larval parasitoid community were analyzed because of the difficulty in correcting for the differing sample sizes between larval and pupal collections due to the low number of pupae collected in many sites. Of necessity, I used spatial replication at differing stages of the host cycle in order to examine the parasitoid community over a full range of host densities. Data were collected from three locations (Fig. 3.1), one with high host density and collapsing populations (Roland & Taylor, 1997), and two with endemic host density (Chapter 2). However, one of the areas from which low density populations were sampled (Blackfoot Grazing Reserve) falls within that area from which outbreak data were collected (the Ministik region) (Fig. 3.1). During outbreaks (1995, 1996), 9017 FTC larvae were collected from 130 sites, while only 143 larvae were collected from 32 sites during the collapse phase of the host cycle. Parasitoid community data from low host densities (2002, 2003, and 2004) were taken from a separate experimental analysis in which experimental outbreaks were created in both forest fragments and continuous forest within two separate grazing reserves (see Chapter 2 for more details). A total of 1808 larvae were collected from 30 sites within the low host density populations.

Rearing methods were identical for both studies. All collected larva were reared in paper bags and fed fresh aspen every 2 days. Larval densities within each bag were kept as low as possible in order to minimize density-dependent rearing mortality. Larvae were reared until healthy FTC adults, or parasitoids emerged. Parasitoids were identified based on characteristics of puparia and of the stigmal plates found on

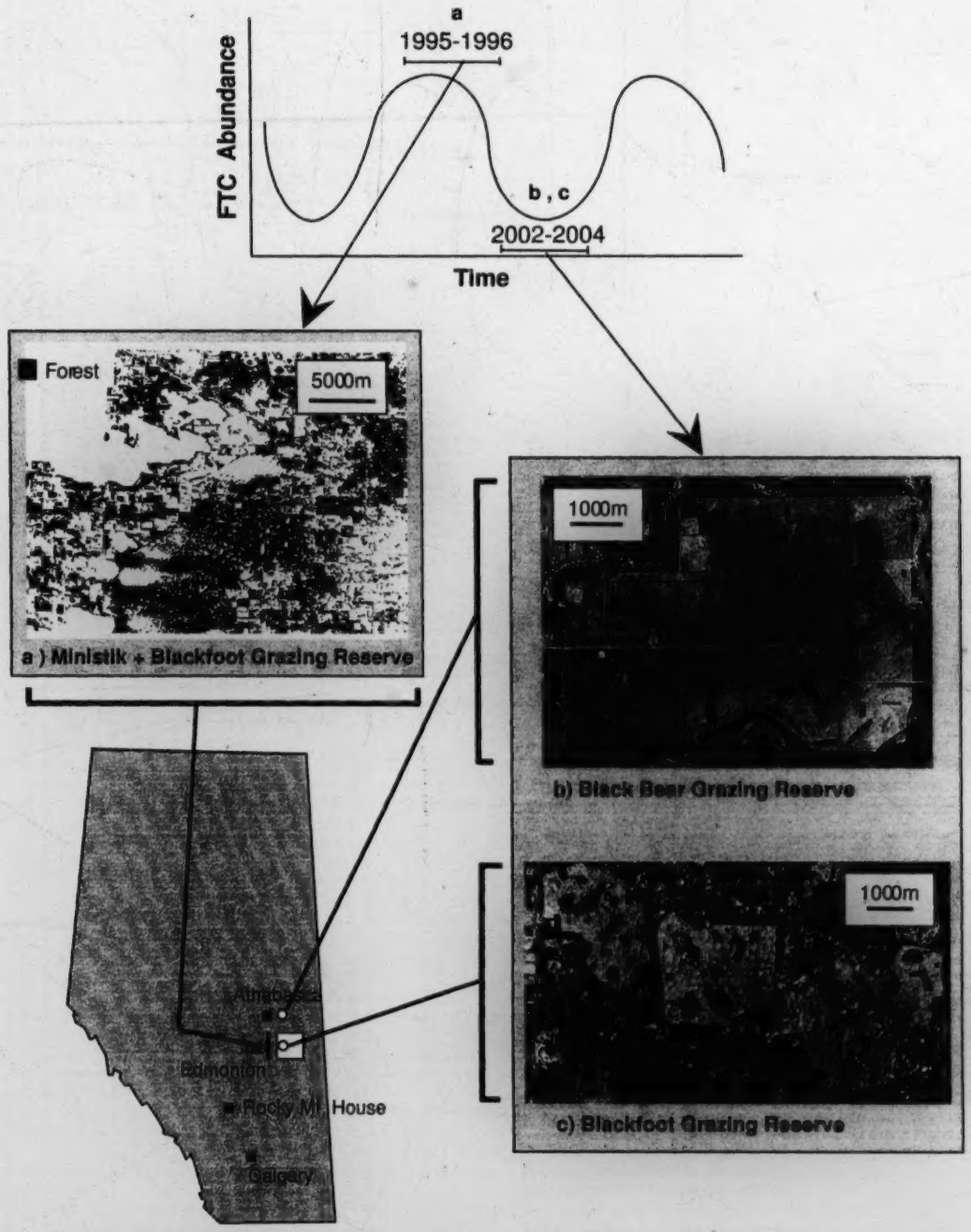

Figure 3.1: Schematic showing that spatial replication was necessary to get full range of host densities. Endemic data were collected from the Black Bear Grazing reserve (10 sites), and the Blackfoot Grazing Reserve (8 sites). Outbreak data were collected from the Ministik area (including Blackfoot Grazing Reserve) near Cooking lake Alberta (130 sites).

the surface of the puparia (Sippel, 1956).

Statistical analysis

The response of the FTC parasitoids community to host density and landscape was examined by using both the Simpson's Index (Magurran, 1988) and the Multi-Response Permutation Procedure (MRPP) (McCune *et al.*, 2002). Simpson's Index was chosen as a measure of species diversity because it is less affected by small sample size than are other diversity indexes (Magurran, 1988), and because it emphasizes the more common species (Krebs, 1999), thereby focusing on the core group of FTC parasitoids that may affect host dynamics. The Simpson (D) was calculated as:

$$D = \sum \frac{\eta(\eta - 1)}{N(N - 1)} \tag{3.1}$$

where η = the number of individuals in a given species, and N=the total number of individuals. I report 1-D, because I wanted an index that increases with increasing diversity (Magurran, 1988). Rarefaction was not used to deal with differences in sampling effort, because of the small differences in the absolute number of species amongst sites.

An MRPP analysis was used to compare community structure between different levels or groups of the factor of interest. MRPP is a non-parametric procedure that tests the hypothesis of no difference between two or more groups, and does not require multivariate normality, nor homogeneity of variances (McCune & Mefford, 1999). This test provides several key statistics. The change-corrected within-group agreement (A) gives an estimate of within group homogeneity compared to the

random expectation, and typically falls below 0.1 for ecological studies (McCune & Mefford, 1999). This statistic can be thought of as the effect size of the factor of interest (McCune & Mefford, 1999). The distance measure provides an estimate of the dispersion within each group, while the P value indicates whether the community structure differs significantly between the groups of interest. It should be noted that one must weigh the apparent effect size versus the P values for all analyses, as it is possible to achieve statistical significance with high sample size, but have the effect size be relatively small and therefore have little ecological significance (McCune *et al.*, 2002). Furthermore, one must visually examine the pattern to truly assess the strength of any of these factors. MRPP analyses are typically carried out between pre-existing groups such as burned and unburned forest. However, in this study I also used the MRPP to analyze community differences between some arbitrarily defined groupings (see analysis of forest fragmentation below). Because of this, a log-linear G-test was also carried out for each of the following comparisons to provide another test with which to determine if the distribution of parasitoids within a complex was independent of the factor of interest.

A single estimate of community composition from each sample (the proportion of each parasitoid species within each sample) was used as the unit of measure for all analyses. For data from the low density host populations, one estimate of community composition was determined for each of my experimental sites in each year (see Chapter 2). For data from the outbreak and collapse populations, one estimate of community structure was made for each point within the 420km^2 grid (Roland & Taylor, 1997).

Significant MRPP analyses were followed by an Indicator Species Analysis. This

test provided a measure of the percent of perfect indication for each species within each group by combining both species abundance, and the frequency with which a species is present within a group (McCune *et al.*, 2002). The indicator value for each species thus gives an estimate of how representative that species is for that particular group; a perfect indicator for a group would be exclusive to that group (McCune & Mefford, 1999). Statistical significance for indicator values was tested using Monte Carlo randomization with 1000 permutations (McCune *et al.*, 2002), and hence P values are based on the proportion of randomized trials in which indicator values were equal to, or exceeded, the observed indicator value (McCune & Mefford, 1999). All MRPP's and indicator species analyses were done using PC-ORD 4.14 (MjM Software, 1999).

The following comparisons were made:

1) **Areas with high host density and areas with low host density**. A single diversity estimate was calculated for each of the following phases of the host cycle; outbreak (1995-1996), collapse (1998), and low host density (2002-2004). The MRPP analysis only compared community structure between high host density populations (1995-1996) and low host density populations (2002-2004), because all sites from the collapse phase had fewer than 10 parasitoids per sample. Only data from the two areas closest to each other (Blackfoot reserve, and the area surrounding Cooking Lake Alberta) were used in order to minimize the effect of geographical location.

Because the area over which the outbreak parasitoid complex was sampled was larger than that of the endemic parasitoid complex, three sub-samples from an area equivalent in size to that of the Blackfoot Grazing Reserve were taken from the Ministik area in order to ensure that any differences in species diversity seen between

high and low density host populations were not caused by differences in sample area. These sub-samples were evaluated separately. Similarly, because the range of forest cover was greater in the area from which the outbreak parasitoid complex was sampled (0-100% forest cover for the outbreak sample area compared to 0-75% for the endemic study area), I also calculated the species diversity of a sub-sample containing only those outbreaks sites with 0-75% forest cover.

2) **Forest fragmentation measured at a scale of 425m^2.** The proportion coverage of forest in the landscape was used as a measurement of forest fragmentation. This was calculated by using 1:40 000 and 1:20 000 air photos, and estimating the number of cells of a 5X5 grid measuring 425m on a side (18ha), that was forested. This scale was chosen because it is known to be intermediate with respect to the scales at which FTC parasitoids assess the landscape (Roland, 2005; Roland & Taylor, 1997).

Sites were grouped by the amount of forest surrounding the site, however the range of forest cover differed between the two data sets, in part because of the greater number of sites within the outbreak data set. For the outbreak data set (Cooking Lake), forest cover ranged from 0-100% forest, and was classified as: 0-25%, 26-50%, 51-75%, and 76-100%. For the low host density data set, the amount of forest surrounding sites ranged only from 0-75%, resulting in only three classes of forest cover; 0-25%, 26-50%, and 51-75%. MRPP analyses are typically carried out between two distinct groups, however, here I used an MRPP to examine differences between these arbitrary groupings in order to keep my methods consistent. The results should thus be interpreted cautiously.

3) **Blackfoot and Black Bear grazing reserves**. These two sites were compared to see if the structure and diversity of parasitoid assemblages differed between geographical locations within Alberta (140 km apart). Because I do not have data from outbreak populations for the Black Bear Reserve, I only examine differences between reserves at low host density. Data from all fragments and continuous forest within each reserve were combined in order to calculate the species diversity estimates. The MRPP analysis was carried out on a total of 22 sites (13 within the Black Bear reserve, and 9 within the Blackfoot reserve (2002, 2003, 2004). Eight sites were excluded because N<10. This comparison was done primarily to determine if there was any strong difference in community structure between reserves which may have biased the previous two analyses.

4) **Forest fragments vs. continuous forest**. This analysis was carried out on 15 fragment-continuous pairings from both the Black Bear and Blackfoot Grazing Reserve during the endemic phase of the cycle (2002 - 2004). Initial analyses were carried out only on sites from the Black Bear Grazing Reserve in order to minimize differences between reserves; however, sample size proved small, and it was felt that a statistically stronger estimate would be obtained using information from both reserves.

Results

Collections

A total of 3647 parasitoids were reared from 10967 fifth-instar larvae. Late larval dipteran parasitoid assemblages were comprised primarily of *C. malacosomae*, *L. frenchii*, *L. exul*, *P. pachypyga*, *E. mella*, and *E. futilis* (Table 3.1). Two additional species, *Achaetoneura melalophae* Allen and *Chaetogena edwardsii* (Williston), were found only during FTC outbreaks, and were therefore not included in those analyses involving low density host populations.

Host density

Parasitoid species diversity was greatest in outbreaking FTC populations, and lowest in collapsing populations. The species diversity estimate for collapsing populations, however, is based on a small sample size relative to that of either the outbreak or endemic host stages, and should be viewed conservatively. These differences in species composition were reflected in the results of the MRPP analysis and the G-test; community structure changed as the host cycle progressed from outbreak (1995-1995), to low host densities (2001, 2002, 2003) (Fig. 3.2, Table 3.2, $G = 1004.94$, df=35, $P<0.001$). The species diversity estimates the sub-sample of sites taken from areas equal in size to that of the Blackfoot Grazing Reserve, however, were similar to the estimate calculated from all samples within the large Ministik area (Table 3.2). This suggests that the greater species diversity in the outbreak parasitoid complex was not due to the larger sample area. Species diversity estimates from the sub-sample of only those sites from the FTC outbreak with 0-75% forest cover was nearly identical to

that from sites within the full range of forest cover (0-100%) (Table 3.2), suggesting that the higher diversity seen in parasitoids complexes from FTC outbreaks was not caused by a greater range of forest cover.

Table 3.2: MRPP analyses and species diversity values for differing stages of the host cycle. For MRPP; N = the number of samples in each group. A = change-corrected within-group agreement. P= significance level for the differences between groups. Outbreak(Sub1-3) represent sub-samples of sites from the outbreak sample area. Each subgroup was comprised of sites from a 12 x 8 km sample area within the larger outbreak sample area (Ministik and Blackfoot Grazing Reserve). Outbreak(SubFragClass) represents a sub-sample of only those sites with 0-75% forest cover. For Simpson index; D = index of diversity. For each analysis, two years of data were combined for each site.

MRPP

Phase of Host Cycle	Average Ranked Distance	N	A	P
Outbreak	0.489	204	0.0463	0.0001
Endemic	0.279	10		

Simpson Index

Phase of Host Cycle	Simpson's D	#of Species	Total # Parasitoids	Total # Hosts
Outbreak (total)	0.713	8	2892	6162
Outbreak (Sub1)	0.710	7	592	1470
Outbreak (Sub2)	0.694	6	659	1721
Outbreak (Sub3)	0.731	7	341	900
Outbreak (SubFragClass)	0.713	8	1787	4453
Collapse	0.337	3	52	143
Endemic	0.623	6	303	1808

During FTC outbreaks, the parasitoid complex was dominated by *P. pachypyga*, *C. malacosomae*, and *L. exul*, whereas *C. malacosomae* was the most dominant species during the collapse (Fig. 3.2). *P. pachypyga* and *L. exul* were virtually absent in low density FTC populations, wheras *L. frenchii* was much more dominant in low density

FTC populations than during outbreaks. The proportion of *L. frenchii* within the assemblage increased from 2002 through 2004, comprising almost 60% of the parasitoid community in the final year of the study (Fig. 3.2). Although the significance of the MRPP analysis may have been elevated because of the high number of samples taken from the FTC outbreak relative to that of either the collapse or endemic phases of the host cycle (McCune *et al.*, 2002), the graphical analysis reveals a strong pattern consistent with past research (Parry, 1995), with a decrease in the abundance of specialist parasitoids, and an increase in the impact of more generalist parasitoids. Furthermore, the G-test revealed a strong effect of host abundance on the distribution of parasitoids within the complex ($G=1004.9$, $df = 35$, $p < 0.0001$). The Indicator Species Analysis revealed that *L. frenchii* and *E. fultilis* are found primarily in endemic host populations, while *P. pachypyga* and *L. exul* are most prominent during host collapse (Table 3.3).

Table 3.3: Results from Indicator Species Analysis for differing phases of the host cycle. Indicator values represent % of perfect indication, based on combination of relative abundance and relative frequency. P values represent the Monte Carlo significance of each observed indicator value based on 1000 randomizations; P values are based on the proportion of randomized trials where indicator values were equal to, or exceeded, the observed indicator value (McCune & Mefford, 1999).

Species	**Outbreak**	**Collapse**	**Endemic**	**P**
L. frenchii	0	0	90	0.0010
A. melalophae	0	0	0	0.8180
C. malacosomae	20	53	23	0.0070
E. futilis	0	0	59	0.0010
E. mella	26	0	1	0.2220
L. exul	51	23	8	0.0140
C. edwardsii	4	0	9	1.0000
P. pachypyga	56	0	9	0.0160
Average	20	9	24	

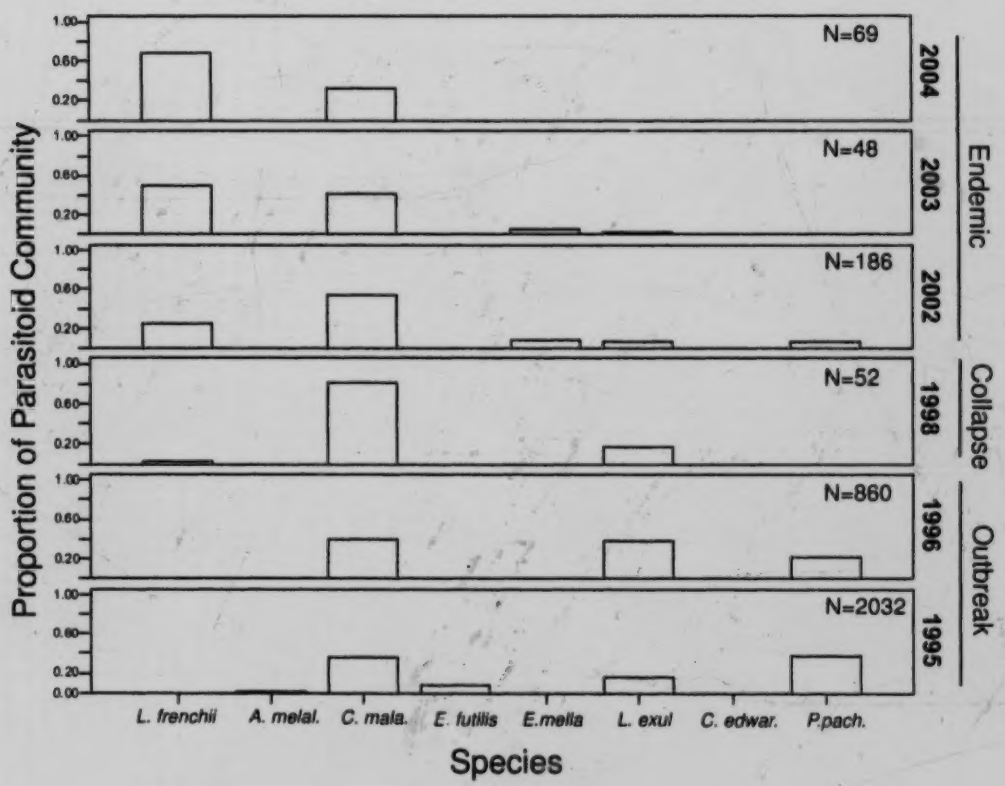

Figure 3.2: Changing community composition of the FTC late larval parasitoid community over a 10 year period in the Cooking Lake region of Alberta. 1995=Initial Outbreak, 1996=Peak Outbreak, 1998=Collapse, 2002-2004=endemic host densities.

Landscape

Fragmentation had a significant effect on the parasitoid community at both high and low host density. The Indicator Species Analysis, however, suggests that no single species is indicative of one class of fragmentation for either outbreak or endemic populations, which might be expected given the arbitrary nature of the groupings. During host outbreak, landscape measured at a scale of 425m had a significant effect on community structure (Table 3.4, Fig. 3.3, G-test: G= 213.44, df=24, $p<0.0005$). The proportion of *P. pachypyga* decreased as the landscape became more fragmented, while *C. malacosomae* showed the opposite pattern, comprising more than 50% of the parasitoid community in highly fragmented landscapes, and only 15% in continuous forest (Fig. 3.3). In contrast, *L. exul* appeared not to be affected by fragmentation at high density, comprising about 25-30% of the parasitoid community in all fragmentation classes. Species diversity was similar in all classes of fragmentation, but was lowest in the highly fragmented forest as was predicted (Table 3.4).

The effect of forest fragmentation on the parasitoid community in endemic host populations was also statistically (Table 3.5) (G=30.33, df=10, P = 0.001), and the effect size (A) of fragmentation was greater in the endemic phase of the host cycle than during outbreaks. The greater statistical significance in outbreak populations likely results from higher sample size. Parasitoid assemblages from low host densities had fewer species than did those from outbreak FTC populations, and only *C. malacosomae* and *L. frenchii* appear to respond to fragmentation (Fig. 3.3). *C. malacosomae* comprised a greater proportion of the parasitoid complex in fragmented forests, while *L. frenchii* showed the opposite pattern, with higher abundance in frag-

mented forest. Interestingly, species diversity estimates from the low host density populations were highest in the most heavily fragmented landscapes, and decreased as the amount of forest within the landscape increased (Table 3.5). Species diversity was nearly identical in forest fragments and continuous forest within low density host populations (Table 3.5). The MRPP analysis indicates that community structure did differ between forest fragments and continuous forest (Table 3.4), however, the G-test contradicted this finding (G = 7.02, df=5, P>0.05). The Indicator Species Analysis suggests that no species were found exclusively in either forest fragments or continuous forest, however, *L. frenchii* was typically found in forest fragments.

Table 3.4: MRPP analyses and species diversity values for the outbreak parasitoid community in landscapes with differing degrees of forest fragmentation. Format as in Table 3.2

MRPP

Percent Forest Cover	Average Ranked Distance	N	A	P
0-25%	0.393	23	0.034	0.0004
26-50%	0.542	32		
51-75%	0.481	36		
76-100%	0.483	44		

Simpson Index

Percent Forest Cover	Simpson's D	# of Species	Total # Parasitoids	Total # Hosts
0-25%	0.628	6	344	861
26-50%	0.724	8	596	1491
51-75%	0.702	7	847	2101
76-100%	0.718	6	646	1709

Table 3.5: MRPP analyses and species diversity values for the low host density parasitoid community in landscapes with differing degrees of forest fragmentation. Format as in Table 3.2

MRPP

Percent Forest Cover	Average Ranked Distance	N	A	P
0-25%	0.607	6	0.079	0.031
26-50%	0.308	7		
51-75%	0.477	9		

Simpson Index

Percent Forest Cover	Simpson's D	# of Species	Total # Parasitoids	Total # Hosts
0-25%	0.830	6	220	350
26-50%	0.606	8	254	818
51-75%	0.518	5	100	290

Table 3.6: MRPP analyses and species diversity values for parasitoid communities in forest fragments and continuous forest. Format as in Table 3.2

MRPP

Structure	Average Ranked Distance	N	A	P
Fragment	0.549	12	0.058	0.031
Continuous	0.373	10		

Simpson Index

Structure	Simpson's D	# of Species	Total # Parasitoids	Total # Hosts
Fragment	0.609	6	429	1002
Continuous	0.605	6	185	806

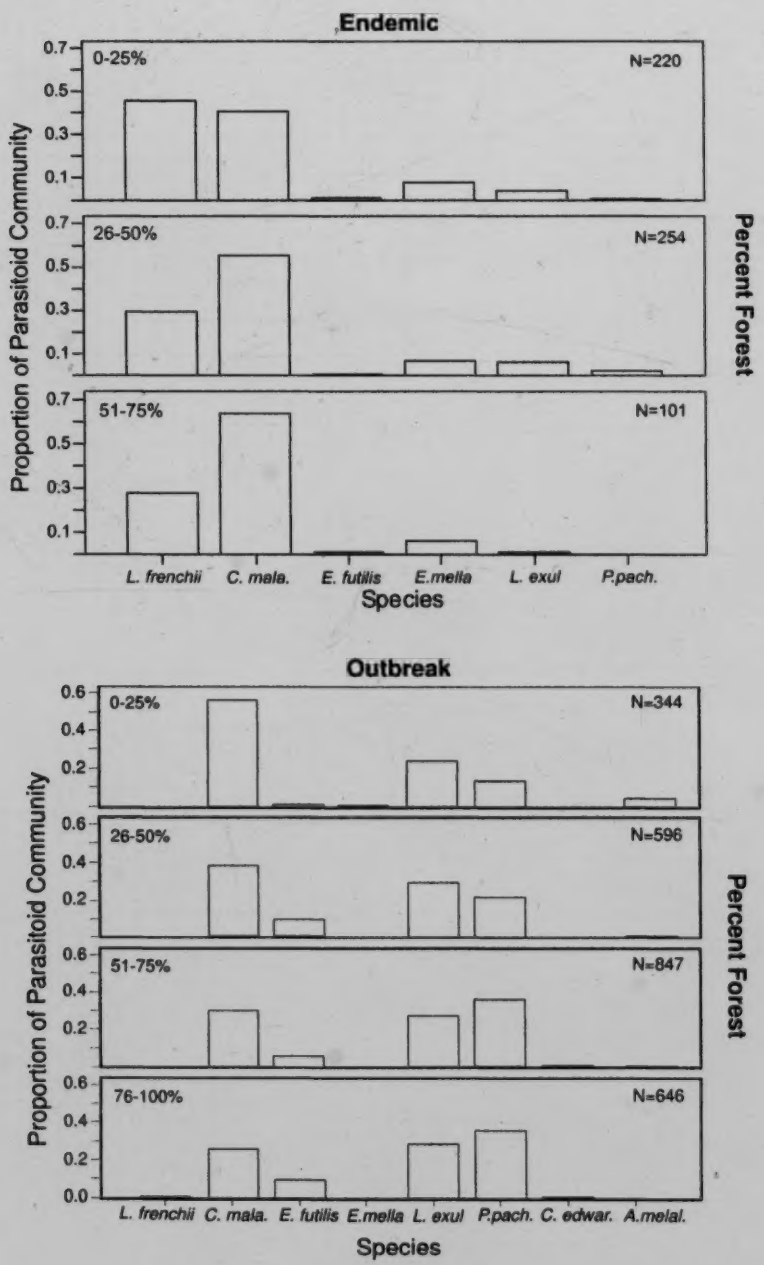

Figure 3.3: Community structure of FTC parasitoid communities from sites with differing levels of fragmentation. N = total number of parasitoids collected.

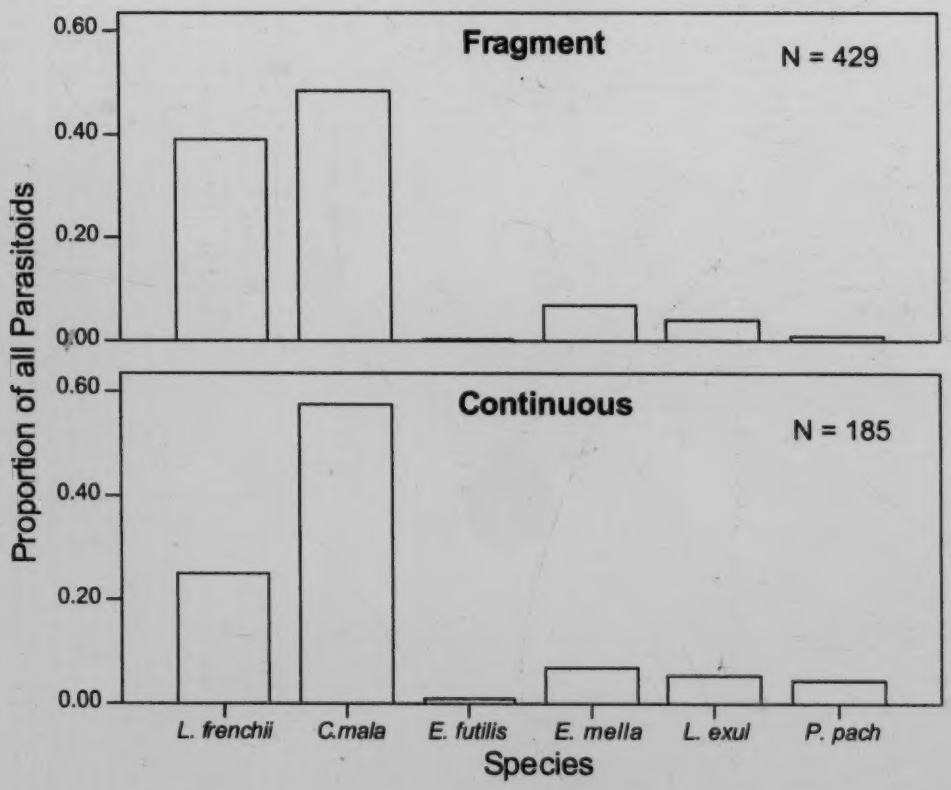

Figure 3.4: Late larval tachinid parasitoid community structure for forest fragments and continuous forest N= total number of parasitoids collected.

Table 3.7: Results from Indicator Species Analysis for the outbreak parasitoid community found in forests with differing degrees of fragmentation. Format as in Table 3.3

	Amount Forest				
Species	**0-25%**	**25-50%**	**50-75%**	**75-100%**	**P**
L. frenchii	0	2	1	0	0.535
A. melalophae	1	0	1	10	0.029
C. malacosomae	17	12	22	35	0.001
E. futilis	0	0	1	1	0.564
E. mella	7	12	11	1	0.305
L. exul	22	25	24	14	0.367
C. edwardsii	2	2	1	0	0.758
P. pachypyga	10	10	9	8	0.010
Average	23	28	24	25	

Table 3.8: Results from Indicator Species Analysis for the endemic parasitoid community found in forest with differing degrees of fragmentation. Format as in Table 3.3

	Amount Forest			
Species	**0-25%**	**25-50%**	**50-75%**	**P**
L. frenchii	59	10	27	0.012
C. malacosomae	38	23	39	0.579
L. exul	1	8	3	0.805
P. pachypyga	27	7	28	0.818
E. futilis	32	1	32	0.476
E. mella	3	0	27	0.213
Average	28	7	26	

Table 3.9: Results from Indicator Species Analysis for the endemic parasitoid community found in forest fragments and continuous forest. Format as in Table 3.3

Species	**Fragment**	**Continuous**	**P**
L. frenchii	73	22	0.011
C. malacosomae	61	39	0.089
L. exul	3	13	0.700
P. pachypyga	49	17	0.226
E. futilis	35	14	0.498
E. mella	12	5	0.875
Average	39	18	

Geographic location

Parasitoid diversity estimates were nearly identical for both the Black Bear Grazing Reserve, and the Blackfoot Grazing Reserve. This similarity was supported by the MRPP analysis (Table 3.10). However, this non-significant finding has likely resulted from a small sample size, as a subsequent G test suggested that the frequency of species did differ between the two reserves ($G = 17.235$, $df=5$, $p<0.01$), primarily because *L. frenchii* was more dominant in the Blackfoot reserve, whereas *C. malacosomae* was more dominant at the more northerly Black Bear reserve (Fig. 3.5).

Table 3.10: MRPP analyses and species diversity values for parasitoid communities in the Black Bear Grazing Reserve, and the Blackfoot Grazing Reserve. Format as in Table 3.2

MRPP

Reserve	Average Ranked Distance	N	A	P
Black Bear	0.420	13	0.046	0.055
Black Foot	0.554	9		

Simpson Index

Reserve	Simpson's D	# of Species	Total # Parasitoids	Total # Hosts
Black Bear	0.597	6	310	725
Blackfoot	0.625	6	304	1808

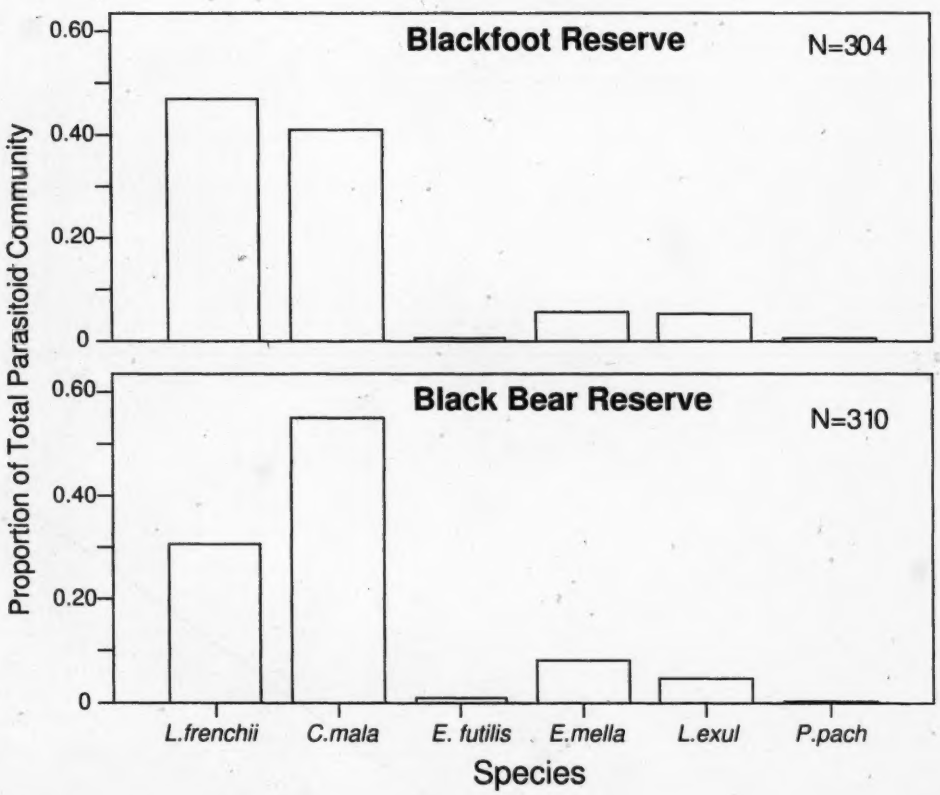

Figure 3.5: Late larval tachinid community structure for both the Blackfoot and Black Bear reserve. Both reserves were at low host densities at the time of these collections. N= total number of parasitoids collected.

Discussion

The makeup of the forest tent caterpillar parasitoid assemblage is affected by both host density and landscape. The response of the parasitoid community to host abundance supported my initial hypothesis; generalist parasitoids comprised a greater proportion of the parasitoid community in endemic host populations than did specialists. Parasitoid communities from both outbreak and endemic host populations were strongly affected by fragmentation, however, pure measures of species richness are unlikely to capture the full nature of this response, because the relative abundance of species is more strongly affected than is the absolute number. The response of parasitoid complexes to forest fragmentation was significant in both outbreak and endemic host populations, although the measure of effect size of forest fragmentation (A) was greater in endemic host populations. Although the mechanisms for the community differences seen in fragmented and non-fragmented landscapes are not known, the similar community structure in both forest fragments and continuous forest (Fig. 3.4) suggests that these effects are unlikely to result from reduced movement of part of the parasitoid community into isolated forest patches, and may instead result from factors such as habitat quality differences, or responses to edge habitat.

The composition of the FTC parasitoid complex found here is consistent with that from previous studies (Parry, 1995; Parry *et al.*, 1997; Roland & Taylor, 1997; Sippel, 1962; Witter & Kulman, 1979), and suggests that FTC parasitoid assemblages are dominated by a core group of species (*L. exul*, *P. pachypyga*, *C. malacosomae*, and *L. frenchii*) which are present in FTC populations throughout the prairie provinces and boreal forests of North America. Variation in species diversity appears to be

determined primarily by the spotty abundance of opportunistic generalist parasitoids such as *E. mella*, *E. futilis*, *A. melalophae* and *C. edwardsii*. Furthermore, the low diversity during the collapse of the host populations is in part determined by the low sample size, and may not reflect the true diversity of this complex. Thus, although there was variation in species diversity, I feel that these differences are unlikely to impact host dynamics. The relative uniformity of the core parasitoid community across the prairies is supported by the non-significant response of parasitoid communities to geographic location. Although the MRPP analysis was nearly significant, and would likely have been with increased replication, community structure of the endemic parasitoid complex differed only in the relative proportions of *C. malacosomae* and *L. frenchii*. This is not to suggest that parasitoid communities will never differ between locales. Parasitism rates can differ between geographic locations for FTC (Parry, 1995) and gypsy moth (Hoch *et al.*, 2001), and the FTC parasitoid communities in the swamps of Alabama are dramatically different from those in the northern prairies and boreal forests (Stark & Harper, 1982). Broad-scale habitat differences undoubtedly result in differential community composition, however, the results of my study suggest that FTC parasitoid community structure is relatively constant across areas of Alberta with similar habitat.

The response of the FTC parasitoid complex to the host cycle appears to be associated with differences in host specificity among parasitoid species, and by the ability of some species to increase numerically in response to host density. Specifically, those specialist parasitoids which numerically increase in response to host density are more prevalent in outbreak host populations, while low density FTC populations are dominated by more polyphagous parasitoids which are able rely in part on other

lepidopteran hosts. Similar patterns in the response of parasitoid communities to host abundance have been reported for gypsy moth (Hoch *et al.*, 2001; Skinner *et al.*, 1993), spruce budworm (Miler & Renault, 1976), and winter moth (Embree, 1966), suggesting that such patterns are common in the parasitoid communities of cyclic host species. In my study, the parasitoid community in outbreak populations was dominated by specialist tachinids *L. exul* (2 alternative hosts) and *P. pachypyga* (3 alternative hosts), and by the more polyphagous *C. malacosomae* (8 alternative hosts). Typically *L. exul* and *P. pachypyga* cause high parasitism during outbreaks as a result of their ability to increase numerically in response to host density by laying hundreds of eggs near ubiquitous caterpillar caused defoliation (Parry, 1995; Parry *et al.*, 1997; Roland & Taylor, 1997; Witter & Kulman, 1979). *C. malacosomae* does not show such a numerical increase, however, and typically has a lower impact during outbreaks than that observed here, with parasitism having been reported as low as 0.5% in some outbreak populations (Parry, 1995) (compared to 25-30% in this study). This high proportion of *C. malacosomae* in this study may result from my inability to detect superparasitism by this species. Although there is no previous record of the frequency with which superparasitism occurs for *C. malacosomae*, up to four larvae can emerge from a single host (Parry, 1995).

The parasitoid complex from low density host populations was characterized by a greater presence of *L. frenchii* relative to that in the outbreak assemblage, and by a decrease in the abundance of both *L. exul* and *P. pachypyga*. Both *L. exul* and *P. pachypyga* are known to have lower parasitism in endemic host populations compared to during outbreaks (Parry, 1995; Parry *et al.*, 2003; Witter & Kulman, 1979). The virtual absence of these two species in endemic host populations in this study, however,

is unexpected given that *L. exul* and *P. pachypyga* can cause parasitism as high as 25% and 50% respectively in some low density host populations (Parry *et al.*, 1997). The limited presence of *L. exul* and *P. pachypyga* in my study may have resulted from an overestimation of the proportions of *C. malacosomae* and *L. frenchii* due to my inability to account for superparasitism (see Chapter 2). Despite this, only 28 *L. exul* and 12 *P. pachypyga* emerged from 1808 larvae collected in endemic host populations compared to 313 *C. malacosomae* and 214 *L. frenchii*. This substantial difference is unlikely to be caused solely by this overestimation, and suggests that the latter two species do comprise a greater proportion of the parasitoid community during low host densities.

The limited impact of *P. pachypyga* and *L. exul* in endemic host populations may also result from the nature of the host dynamics within the study area. Areas with frequent outbreaks provide a more constant source of hosts with which to support specialist parasitoids, whereas areas with infrequent outbreaks will have a greater proportion of generalist parasitoids which are able to survive on alternative hosts (Hoch *et al.*, 2001). The low proportion of specialists (*L. exul* and *P. pachypyga*) in endemic host populations in my study relative to those of previous studies on FTC (Parry, 1995), may be because of the long interval between host outbreaks; the Black Bear Grazing Reserve has not had an FTC outbreak since 1988 (17 years). Both *L. exul* and *P. pachypyga* are particularly susceptible to extended periods of low host density because their mode of attack requires hosts to ingest eggs which are laid on feeding-damaged aspen foliage (Fitzgerald, 1995; Mondor & Roland, 1997, 1998; Roland & Taylor, 1997; Williams *et al.*, 1996). This mode of attack is inefficient when host densities are low, because larvae are sparsely distributed within the environment,

and because there is a large quantity of non-feeding damaged aspen for larvae to feed on. This is contrasted by high density host populations in which the majority of leaves will have feeding damage, and hence, will likely have parasitoid eggs attached to their surface. This inefficiency of these specialists in low density host populations may result in FTC outbreaks being particularly severe following extended periods of low host density because of the attendant deficit of specialist parasitoids.

Whereas the role of *L. exul* and *P. pachypyga* within the parasitoid complex is relatively consistent among previous studies (Parry, 1995; Parry *et al.*, 1997; Roland & Taylor, 1997; Sippel, 1962; Witter & Kulman, 1979; Williams *et al.*, 1996), the exact role of *L. frenchii* is less clear. Although this species was at one time suspected of being important in endemic populations (Sippel, 1956; Witter & Kulman, 1979), more recent studies indicate that *L. frenchii* is rare at low density (Parry, 1995; Parry *et al.*, 1997) and most prevalent during both the beginning (Witter & Kulman, 1979) and end of outbreaks (Parry, 1995). In my study *L. frenchii* was second only to *C. malacosomae* in abundance in low density host populations. Unfortunately, my results do little to establish whether this species is more prevalent in endemic, or increasing, host populations because the host densities in this study are likely on the cusp between true endemic populations, and the early stages of a new outbreak. My work therefore suggests that while *L. frenchii* is at least present during the endemic phase of the host cycle, its impact increases during the early stages of host outbreaks. The variation in the response of *L. frenchii* to host abundance may result from this parasitoid being extremely polyphagous (Schmidt, 2001), and from its having two generations per year, only one of which uses FTC as a host (Williams *et al.*, 1996). Because of this, the distribution of this species is perhaps more strongly affected

by the distribution of other lepidopteran species (See Chapter 2), and only weakly responsive to FTC abundance.

The response of the FTC parasitoid assemblage to changing host abundance may be confounded by the use of data from studies using different methods. Outbreak data (1995, 1996, and 1998) were from a descriptive landscape study, while data from endemic host populations were from a study using experimentally elevated host densities, resulting in the presence of a strong density gradient. The high proportions of *L. frenchii* and *C. malacosomae* from areas with elevated host abundance against a background of low density could occur if these two species respond spatially to localized areas of high host density, while other parasitoids do not. Within-generation spatial responses to locally elevated host populations are exhibited by generalist parasitoids of gypsy moth in both in Europe (Hoch *et al.*, 2001), and in the United States (Elkinton *et al.*, 1990; Gould *et al.*, 1990). Similar work on FTC parasitoids, however, suggests that unlike *P. pachypyga*, neither *L. frenchii*, nor *C. malacosomae*, exhibit spatial density-dependent responses to elevated host density (Parry *et al.*, 1997). This, coupled with the fact that the patterns of community change observed here (the decrease in specialist parasitoids in endemic host populations) are consistent with past research on forest defoliators (Embree, 1966; Elkinton *et al.*, 1990; Miler & Renault, 1976; Parry, 1995; Skinner *et al.*, 1993; Williams *et al.*, 1996; Witter & Kulman, 1979), suggests that this response is unlikely to be an artifact caused by the experimental methods.

The response of FTC parasitoids to landscape is well documented (Roland, 1993; Roland & Taylor, 1997; Roland, 2000), and my results further support these previous studies. Fragmentation had a significant effect on parasitoid communities in both

outbreak and endemic host populations. The response of parasitoids to fragmentation has been attributed to inhibited movement in fragmented landscapes (Roland & Taylor, 1997; Roland, 2000), however, the results of Chapter 2 indicate that these differences are not due to differential movement in forest versus clearings. The limited impact of patch isolation on movement is supported by similar species composition in both forest fragments and continuous forest in endemic host populations. Despite the significant result from the MRPP analysis, a visual examination of the relative abundance of parasitoids in forest fragments and continuous forest shows the parasitoid communities to be similar (Fig. 3.4). Although the proportion of *L. frenchii*, *C. malacosomae*, and *P. pachypyga* do vary between the two landscape types, we do not see any species present in continuous forest, and not so in forest fragments. It thus appears that the response of FTC parasitoids to forest fragmentation is not driven by inhibited colonization of isolated habitat patches as seen in other systems (Kruess & Tscharntke, 1994), but may instead result from more subtle responses to such factors as altered microclimate (Saunders *et al.*, 1991) or forest boundaries (see Chapter 2). Unfortunately my study lacks the replication and fine-scale data necessary to reflect on the nature of these fine-scale effects.

Parasitoid complexes from high and low density host populations were hypothesized to differ in the strength of their response to fragmentation because the fine grained habitat requirements of specialist parasitoids may not be met in small patches (Russell, 1989; Tscharntke *et al.*, 2002), and may therefore make the parasitoid complex from host outbreaks more susceptible to fragmentation. Both communities responded significantly to fragmentation, and although the outbreak parasitoid complex did show a more statistically significant response to fragmentation, it is likely due to

the greater number of samples taken from outbreak populations (Table 3.5). This unbalanced design (greater sample size in outbreak populations) therefore limits the inferences I can make regarding the relative strength of the response shown by outbreak and endemic parasitoid communities. The nature of the community change, however, does suggest that the mechanisms responsible for the community response to fragmentation may differ in the two complexes. In outbreak populations, the proportion of *P. pachypyga* decreased with increasing fragmentation, while the proportion of *C. malacosomae* increased. This response of *P. pachypyga* is consistent with that shown by Roland & Taylor (1997), who suggested that the negative impact of fragmentation on this species may result from interference of its density dependent response to hosts. Interestingly the response of *C. malacosomae* to fragmentation in endemic host populations was opposite that seen in outbreaking populations, as it comprised a higher proportion of the endemic parasitoid community in the less fragmented forest. This variable response of *C. malacosoma* supports the suggestion of Parry (1995) that the impact of this species within the parasitoid community is in part determined by the presence of other parasitoids, specifically *P. pachypyga*. Although *C. malacosomae* and *L. frenchii* can emerge from hosts parasitized by *L. exul*, they seldom do so from hosts also parasitized by *P. pachypyga*. This suggests that *P. pachypyga* larvae are able to out-compete the larvae of both *C. malacosomae* and *L. frenchii* (Parry, 1995). Thus, *C. malacosomae*'s apparent positive response to fragmentation in outbreaking host populations, and the high proportion of both *C. malacosomae* and *L. frenchii* in the endemic parasitoid assemblage, may stem in part from competitive release from the absence of *P. pachypyga*.

Within the endemic parasitoid complex, I believe that the higher proportion of

L. frenchii in fragmented forest may result from this species' greater parasitism in forest fragments (Chapter 2). If *L. frenchii* shows greater parasitism and a higher frequency of superparasitism in forest fragments because of reduced emigration out of a patch, it may comprise a greater proportion of the parasitoid community as measured here. It is also possible that the pattern here stems not from a direct response to fragmentation *per se*, but from an indirect response to the distribution of alternative lepidopteran species. That is, during the endemic phase of the FTC population cycle, the distribution of parasitoids is likely to be strongly reflective of the distribution of other host species (Stireman & Singer, 2002). Unfortunately, my study lacks information on the abundance and distribution of other lepidopteran species, and I am therefore unable to provide support for this hypothesis.

The effects of fragmentation on parasitoid community structure may also reflect a difference between the scale at which I measured fragmentation, and the scale at which parasitoids assess the landscape. The effect of landscape on insect diversity is scale-dependent both for Lepidoptera (Hamer & Hill, 2000) and for bees and wasps (Steffan-Dewenter, 2002). This is also the case for FTC parasitoids. Parasitoids respond to landscape in a size-dependent fashion, with smaller parasitoids responding to landscape at smaller spatial scales than do larger parasitoids (Roland & Taylor, 1997). Specifically, parasitism by FTC parasitoids was most responsive to fragmentation measured at the following scales: *C. malacosomae* at 53m, *P. pachypyga* at 212m, and *L. exul* at 850m (Roland & Taylor, 1997). Although Roland & Taylor (1997) did not look at data for *L. frenchii*, it is similar in size to *C. malacosomae*, and might therefore respond to landscape at a small spatial scale. These findings suggest that I have only captured a small part of the full nature of the parasitoid

community response to fragmentation, and further suggests that *L. exul*'s limited response to forest fragmentation in my study may result from measuring fragmentation at a scale smaller than that at which it typically responds. Conversely, I may not be measuring the true effects of fragmentation on *C. malacosomae* or *L. frenchii* either because I have measured fragmentation at a much larger scale than that at which these species respond most strongly.

In conclusion, the findings presented here combined with results from previous studies of FTC parasitoids, suggest that the composition of the FTC tachinid parasitoid complex is characterized primarily by a core group of species (*L. exul*, *P. pachypyga*, *C. malacosomae*, and *L. frenchii*) which are present in FTC populations throughout the prairie provinces. Variation in parasitoid species diversity is relatively low, and is determined primarily by the spotty abundance of opportunistic generalists such as *E. mella*, *E. futilis*, *A. melalophae* and *C. edwardsii*. The relative abundance of the core parasitoid species varies temporally through the host population cycle, as well as responding to the amount of forest within the landscape. Although it is difficult to infer the mechanisms responsible for the effects seen here, it does appear that variation in the response of *C. malacosomae* (and to a lesser extent *L. frenchii*) may stem from competitive release from *P. pachypyga*. Although the response of outbreak and endemic parasitoid assemblages to fragmentation was hypothesized to differ in strength depending upon host density, no such difference was apparent in my results. However, I believe this study may have lacked the statistical power to truly tease apart any differences if they do exist because of the small number of samples taken from endemic host populations relative to outbreak populations. Further work is needed to examine this interaction, as the relationship between the parasitoid response to frag-

mentation at high and low host densities may help us understand the causes behind differential host dynamics in locations with differing landscapes (Roland, 1993). I also feel that further work is needed to examine how parasitoid assemblages differ depending on the history of FTC outbreaks within an area; differences in the frequency or duration of FTC outbreaks can affect the nature of parasitoid assemblages, subsequently affecting the severity of future outbreaks. Finally, although it is difficult to generalize to other host-parasitoid systems because of the nature of the species specific responses, the results point to the importance of examining the effects of fragmentation on host-parasitoid systems of cyclic defoliators not only across varying spatial scales, but also across a range of host densities.

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Chapter 4

Conclusion

Within the prairies of Alberta, the species composition of the FTC dipteran parasitoid community is relatively constant, and is dominated by a core group of species including *Leschenaultia exul* (Townsend), *Patelloa pachypyga* (Aldrich and Webber), *Carcelia malacosomae* Sellers, *Lespesia frenchii* (Williston), and *Arachnidomyia aldrichi* (Parker). Variation in species diversity between locations is primarily determined by the spotty abundance of opportunistic generalist parasitoids such as *Exorista mella* (Walker), *Euexorista futilis* (Osten Sacken), *Achaetoneura melalophae* Allen and *Chaetogena edwardsii* (Williston). However, these species are found only low numbers, and are unlikely to have any effect on host dynamics. Although the core FTC parasitoid complex does not differ significantly between locations with similar habitat, the relative abundance of parasitoids differs markedly depending on the phase of the host population cycle. Parasitoid assemblages from high density host populations contain a large proportion of specialist parasitoids able to increase numerically in response to host density (*L. exul* and *P. pachypyga*). This is contrasted with parasitoid communities from low density host populations, which are dominated by more polyphagous species such as *C. malacosomae* and *L. frenchii* which may survive on alternative lepidopteran species.

Both outbreak and endemic complexes responded significantly to the degree of forest fragmentation in the landscape. Reduced parasitism in fragmented forests (Roland & Taylor, 1997) may result in FTC outbreaks lasting longer (Roland, 1993). The exact mechanism responsible for reduced parasitism, however, remains unknown, but it has been suggested that host populations within forest fragments may become decoupled from parasitoids due to reduced parasitoid movement through forest clearings (Roland, 1993). My results, however, suggest that the effect of fragmentation on

parasitism is not caused by reduced parasitoid movement into isolated forest patches. Neither overall larval, nor pupal parasitism, was higher in continuous forest than in forest fragments. Parasitism by *C. malacosomae* and *A. aldrichi* did not differ between forest fragments and continuous forest, whereas *L. frenchii* parasitism was in fact higher in forest fragments. Neither the isolation distance to the nearest continuous forest, nor the connectedness of the landscape surrounding the patch, had any impact on parasitism for the three species. Furthermore, the relative abundance of parasitoids within the endemic parasitoid complex was similar in forest fragments and continuous forest, and species diversity was nearly identical in the two landscape types. I feel this provides evidence that the majority of FTC parasitoids are able to move throughout the fragmented landscape and into isolated forest patches, at least at the scale studied here.

Increased parasitism by *L. frenchii* in forest fragments may seem counter intuitive, however, I believe this pattern has resulted from this species potentially exhibiting a negative response to patch boundaries. *L. frenchii*'s movement out of a fragment may be inhibited by forest edge, resulting in greater search time per unit area within the patch, and hence, repeated encounters with previously attacked host colonies. This may lead to both elevated parasitism, and an increase in the frequency of multiple parasitism within forest fragments. Such a mechanism has not been reported for this species, although it has been suggested as a possible mechanism for similar patterns exhibited by another FTC parasitoid, *Aleiodes malacosomatos* (Mason) (Roland, 2000). Although parasitism by *L. frenchii* was not affected by proximity to forest edge or patch size, this does not necessarily refute the hypothesis of reduced movement out of a patch, as detection of these subtle responses to forest edge may

require direct observation of parasitoid movement. Avoidance of patch boundaries may appear contradictory given that I've previously stated that parasitoids are able to colonize isolated forest fragments. This pattern reflects the fact that parasitoid movement while foraging for hosts is different from parasitoid dispersal between habitat patches. That is, cues which are known to inhibit insect movement while foraging can be repressed when undergoing long distance dispersal (Kennedy, 1975).

The ability of FTC parasitoids to move through fragmented forest implies that parasitoids are not restricted to certain areas of the landscape, and that parasitism should reflect other factors, such as habitat quality rather than fragmentation. None of the parasitoid species, however, showed a significant response to either *Shepherdia canadensis* (nectar source), aspen (the plant on which FTC feed), or canopy cover (the structural makeup of the forest). This does not eliminate the potential of habitat characteristics to affect parasitism, however, as my study was not designed to accurately examine habitat preference, and my three habitat variables are unlikely to accurately reflect the true nature of the habitat.

The limited effect of landscape and habitat raises the possibility that certain parasitoids may not be responding directly to fragmentation, but indirectly to other factors such as reduced competition in fragmented landscapes, or the distribution of other host species. Although parasitoid communities from both high and low density host populations were found to respond to fragmentation, I believe that the mechanisms responsible for these effects may differ. In outbreak host populations, we see a pattern whereby *P. pachypyga* decreased, and *C. malacosomae* increased, in fragmented forest. The response of *P. pachypyga* is consistent with that shown by Roland & Taylor (1997), who suggested that the negative impact of fragmentation on this

species may result from interference of its otherwise density dependent parasitism of its hosts. Interestingly, *C. malacosomae* showed the opposite response to fragmentation in endemic host populations that it did in outbreak populations, comprising a greater proportion of the community in continuous forest when host densities were low. *P. pachypyga* is known to outcompete both *C. malacosomae* and *L. frenchii* (Parry, 1995). The higher proportion of *C. malacosomae* in fragmented forest during FTC outbreaks is therefore likely a result of competitive release from *P. pachypyga*. This may also partially explain the abundance of *C. malacosomae* and *L. frenchii* in endemic host populations in which *P. pachypyga* is rare. Thus, although fragmentation may not impact the majority of FTC parasitoids directly, it may indirectly affect the community through the response of a single key parasitoid such as *P. pachypyga*.

In endemic host populations, I believe that the distribution of alternative hosts may play a large role in determining parasitism. When FTC densities are low, hosts are more patchily distributed in the landscape. The distribution of parasitoids therefore are less reflective of FTC abundance than of abundance and distribution of other lepidopteran species. The effects of fragmentation on the parasitoid complex in endemic host populations may therefore stem from an indirect response to the distribution of alternative hosts. This is especially relevant for *L. frenchii*, which has approximately 50 other lepidopteran host species (Schmidt, 2001).

In conclusion, my study provides further support for the impact of fragmentation on FTC parasitoids. The results however, suggest that the mechanism responsible for these effects is not reduced parasitoid movement into isolated forest patches, at least at relatively fine spatial scales. My study does not provide a clear alternative mechanism through which fragmentation can affect parasitoids, but does suggest that

the mechanisms responsible may differ depending on the phase of the host population cycle, and point towards the importance of such factors as the parasitoid response to edge habitat, competition among parasitoids species, and the effects of fragmentation on alternative lepidopteran hosts.

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